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Individual variations in energy expenditure and intake

By J. M. Harries, Elizabeth Anne Hobson and Dorothy F. Hollingsworth, *Ministry of Agriculture, Fisheries and Food, Great Westminster House, Horseferry Road, London, S.W.1*

Introduction

Our interest in this subject arises from a desire for information on individual variation in energy requirements, on the proportion of a population needing more and the proportion needing fewer calories than any stated estimate of its average energy requirements. We should like to be able to compare an array of intakes of energy of individuals with a corresponding array of their energy requirements and so to determine what proportion, if any, of the population might be at risk.

Variations between individuals are to be expected and are known to exist: for example, wide variations in energy intake between individual adults were found in the prewar surveys of Widdowson (1936) on men and of Widdowson & McCance (1936) on women. Widdowson (1947) also found great variation in the energy intake of children and she discussed possible causes. Rose & Williams (1961) have shown wide variations in the calorie intakes of male students of the same weight and, apparently, similar activity. Nevertheless, lack of knowledge on the precise extent of variation between individuals makes it necessary to use mean requirements, with their obvious limitations, in assessing the adequacy of diets. In discussing this unfortunate necessity, Orr & Leitch (1937–8) reminded their readers that requirements 'are average values so that in practice, especially when *individual* requirements have to be considered, a margin must be allowed'. Recently, Sukhatme (1961) has drawn attention to the limitations of using average requirements, particularly for assessing inadequate diets or estimating the extent of world food shortage.

In the early studies on energy needs it was usual to measure dietary intake, to consider it in relation to the occupation and other characteristics of the individuals concerned and so to arrive at an estimate of need. For example, Greenwood & Thompson (1917–18) considered the energy yield of daily diets and estimates of the cost of certain activities in determining the needs of the 'average man' for an 'average' day's work. Another way of tackling the problem is to measure energy expenditure, and attempts have been made to do it by various means. One way is to sum the energy needed for basal metabolism, the extra energy needed for daily activities and an allowance for the specific dynamic action of foods (cf. Orr & Leitch, 1937–8). Another way is to record the time spent by individuals on each and all the separate activities that make up daily life, to measure the energy cost of each activity and from both to calculate the total daily expenditure (cf. Passmore & Durnin, 1955; FAO: Second Committee on Calorie Requirements, 1957). Yet another way is to use an instrument such as the integrating motor pneumotachograph or IMP (Wolff, 1956) to measure integrated energy expenditure over long periods. Provided that an adult is neither gaining nor losing weight, intake and expenditure must balance. For groups, balance between mean intake and expenditure is usual for experiments lasting no longer than a week, but is rarely achieved for individuals in so short a time (Durnin 1961*a*,*b*). Durnin (1961*a*) concluded that 'the mechanism whereby our appetite is satisfied is by no means nicely adjusted to expenditure of energy'. For a growing child balance between intake and expenditure is not to be expected and energy intake gives the better estimate of need.

Our aim was to study variation in daily energy requirements, and it seemed that to do so we could use records of expenditure measured by any method in common use or records of dietary intake, in spite of the physiological complexities that arise in their interpretation. To achieve the array we needed, any such records had to exist for a sufficiently large number of individuals.

Many observations of basal metabolism have been made and information on individual variations is available. Harris & Benedict (1919) reported that the coefficient of variation in a sample of about 100 adults was about 12% and that when individual differences in weight, height and age were allowed for by multiple correlation techniques, the coefficient of variation was about 6%. Orr & Leitch (1937–8) considered that much of this apparent variability was due to external circumstances and that the real variation was probably very small. Robertson & Reid (1952) measured the basal metabolic rates of 987 males and 1323 females, aged 3–80 years and reported results for each year of age from 3 to 40 and at older ages for 5-year age groups. They calculated coefficients of variation for each of the age groups and found values ranging from 2·4% to 11·9%, but apparently not systematically with age or sex. By their choice of unit of measurement, Robertson & Reid allowed for individual differences in body size, so that their estimates are comparable with the 6% value of Harris & Benedict.

In much of the literature on the energy cost of separate activities, mean values only are quoted and many investigations have been devoted to a small number of individuals engaged in a multitude of activities. Nevertheless, by pooling the observations of many workers it might be possible to calculate coefficients of variation for such common activities as sitting, standing and walking, though we have not attempted to do that. The cost of an activity such as walking has been shown to be more closely related to body-weight than to any other variable (Mahadeva, Passmore & Woolf, 1953). The coefficients of variation of body-weight of 27 515 adult males and 33 652 adult females in 1943 were 16% and 17% respectively (Kemsley, 1950). The variances were smaller for younger than for older adults.

In the study now reported we have collected estimates showing the magnitude and form of possible variations in both daily energy expenditure and intake, using published and unpublished results from surveys of energy expenditure and intake

Table 1. *Variations in energy expenditure*

Source	No. of subjects	Period of survey (days)	Information about subjects	Mean daily value for all subjects (kcal)	Minimum daily mean for any subject over the period (kcal)	Maximum daily mean for any subject over the period (kcal)	Standard deviation of subject means (kcal)	Coefficient of variation of subject means (%)
Happold (1945)	29	—	Medical students (♂)					
			November	2609	—	—	281	10·8
			January	2640	—	—	225	8·5
	20	—	Medical students (♀)					
			November	2349	—	—	186	7·9
			January	2409	—	—	263	10·9
Edholm, Fletcher, Widdowson & McCance (1955)	6	14	Intermediate cadets	3488	2991	4099	327	9·4
	6	14	Junior cadets	3343	2972	3652	270	8·1
Garry, Passmore, Warnock & Durnin (1955)	10	7	Clerks	2800	2330	3290	353	12·6
	19	7	Miners	3660	2970	4560	459	12·6
Adam, Best, Edholm & Woolf (1957)	13	4	Army troops: exercise I	3429	3124	3952	230	6·7
	13	5	exercise II	4923	4252	5554	370	7·5
	13	5	exercise III	3224	2897	3459	161	5·0
Booyens & McCance (1957)	4	7 or	Scientific workers: ♂	2797	1933	3897	597	21·3
	2	14	♀	2054	1438	2593	—	—
Durnin, Blake & Brockway (1957)	12	7	Housewives	2090	1764	2320	164	7·8
	12	7	Their daughters	2255	1819	2848	282	12·5
Adam, Best, Edholm, Fletcher, Lewis & Woolf (1958)	29	21	Army recruits	3774	2868	4765	444	11·8
Adam, Best, Edholm, Goldsmith, Gordon, Lewis & Woolf (1959)	5	18	Army recruits	3764	3499	4105	251	6·7
Durnin, Blake, Brockway & Drury (1961)	15	7	Elderly women	1991	1492	2409	251	12·6
Durnin, Blake, Allan, Shaw & Blair (1961)	20	7	Elderly women	2290	1795	2962	299	13·1
Durnin, Blake, Allan, Shaw, Wilson, Blair & Yuill (1961)	33	7	Elderly industrial workers ♂	2957	2185	3958	486	16·4
Blake, Durnin, Aitken, Caves & Yuill (1962, in preparation)	9	7	Elderly retired ♂	2327	1754	2811	322	13·8

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of individuals, calculating these, where necessary. So that these might later be used to assess variations in energy requirements, we have used, as far as possible, homogeneous groups by age and sex, and since many inquiries have dealt with occupational groups this has inevitably meant some homogeneity of activity. We have confined the exercise to British data, partly to keep it to manageable proportions and partly so that we could have the benefit of the personal advice of the workers whose data we have used. We often had to estimate the measures of variation shown in the tables, to a degree of accuracy dependent on the data available. We have produced no new experimental observations of our own.

Energy expenditure

Our object was to assess the variation between individuals in the total daily expenditure of energy, and Table 1 shows the collected estimates of these variations. Energy requirements are known to vary with body size and composition, age, sex, activity and climate (cf. FAO: Second Committee on Calorie Requirements, 1957). No attempt has been made, in compiling Table 1, to distinguish persons of different body size and composition; in some, but not all, of the studies there was uniformity of age; all groups are of one sex and most are of like occupation and therefore may be of similar degrees of activity. All the studies were made in the UK and therefore climate is unlikely to have been an important cause of variability. The variations are likely to reflect differences in body size and composition and to some extent differences in age and activity.

The data included are not entirely comparable. For example, in the studies of Edholm, Fletcher, Widdowson & McCance (1955), Adam, Best, Edholm & Wolff (1957), Adam, Best, Edholm, Fletcher, Lewis & Wolff (1958) and Adam, Best, Edholm, Goldsmith, Gordon, Lewis & Wolff (1959) the subjects were of similar age and were all engaged in like activities; therefore, the estimates of variation are probably low. On the other hand, the estimate from the study of Booyens & McCance (1957) may be abnormally high, for the reason that its six subjects (four males and two females) were deliberately chosen because their basic metabolic rates were at the extremes of the range for twenty-two possible male and fourteen possible female subjects. It is clear that the data in Table 1 are too sparse to permit any firm estimate of the individual variation of energy expenditure within age–sex groups. The estimates, however, probably represent the limits, the true coefficient of variation lying somewhere between 10 and 20% of the mean values found; for age–sex–occupation groups it is likely to be nearer 10%.

Energy intake

The only data suitable for our purpose were those representing the food intake of individuals, and we made a critical review of all British surveys on individuals. To reduce the risk of reporting variations resulting from different methods of survey, weighed individual dietary surveys continued for a minimum of 7 days form the basis of the results shown in Tables 2, 3 and 4, for adult males, adult females, and children and adolescents respectively. All the subjects included had a

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Table 2. *Variations in energy intake: adult males*

Source	No. of subjects	Period of survey (days)	Information about subjects	Mean daily value for all subjects (kcal)	Minimum daily mean for any subject over the period (kcal)	Maximum daily mean for any subject over the period (kcal)	Standard deviation of subject means (kcal)	Coefficient of variation of subject means (%)
Widdowson (1936)	63	7	Various, middle class	3067	1772	4955	714	23·3
Happold (1945)	29		Medical students: November	2674	—	—	695	26·0
			January	2713	—	—	526	19·4
Pyke, Harrison, Holmes & Chamberlain (1947)	12	7	Active aged (in small institution)	2160	2050	2251	66	3·1
	12	7	Infirm aged (in large institution)	2069	1903	2272	100	4·8
Bransby, Daubney & King (1948–9*b*)	15	3	(By calculation)	2306	1907	2796	243	10·5
			(By analysis)	2223	1849	2727	260	11·7
Kitchin, Passmore, Pyke & Warnock (1949)	61	7	Students: at home	3040	2140	4690	580	19·1
	47	7	in lodgings	2900	2150	3870	470	16·2
	19	7	in hostel	2960	2440	3590	290	9·8
Ministry of Food (1949, unpublished)	74	7	Industrial workers	3407	2108	4470	511	15·0
Bransby & Osborne (1953)	125	7	Elderly	2096	< 1000	> 3000	503	24·0
Bransby (1954)	152	7	Industrial workers	3549	—	—	620	17·5
Edholm, Fletcher, Widdowson & McCance (1955)	6	14	Intermediate cadets	3524	2917	4222	407	11·5
	6	14	Junior cadets	3340	2832	4085	348	10·4
Garry, Passmore, Warnock & Durnin (1955)	19	7	Miners	4030	3090	5410	557	13·8
	10	7	Clerks	3040	2500	3830	412	13·6
Adam, Best, Edholm & Woolf (1957)	13	4	Army troops: exercise I	3502	2998	4130	370	10·6
	13	5	exercise III	5026	4374	6116	526	10·5
Booyens & McCance (1957)	4	7–14	Scientific workers	2868	2133	4412	676	23·6
Adam, Best, Edholm, Fletcher, Lewis & Woolf (1958)	58	21	Army recruits	3818	2027	5333	625	16·4
Adam, Best, Edholm, Goldsmith, Gordon, Lewis & Woolf (1959)	6	18	Army recruits	4077	3459	4563	415	10·1
Cook & Wilson (1960, private communication)	561	7	Students	2984	—	—	507	17·0
Heady, Marr & Morris (1961, unpublished)	118	7	Bank officials	2851	1749	4055	430	15·1
Durnin, Blake, Allan, Shaw, Wilson, Blair & Yuill (1961)	33	7	Elderly industrial workers	2993	2119	3963	376	12·6
Blake, Durnin, Aitken, Caves & Yuill (1962, in preparation)	9	7	Elderly retired	2054	1406	2606	398	19·4

Table 3. *Variations in energy intake : adult females*

Source	No. of subjects	Period of survey (days)	Information about subjects	Mean daily value for all subjects (kcal)	Minimum daily mean for any subject over the period (kcal)	Maximum daily mean for any subject over the period (kcal)	Standard deviation of subject means (kcal)	Coefficient of variation of subject means (%)
Widdowson & McCance (1936)	63	7	Various, middle class	2187	1453	3110	388	17·7
Andross (1936)	109	3–5	Students	2035	—	—	371	18·2
Widdowson & Alington (1941)	57	7	Various, middle class	2137	—	—	420	19·7
Happold (1945)	20		Medical students: November	2348	—	—	449	19·1
			January	2346	—	—	435	18·5
Pyke, Harrison, Holmes & Chamberlain (1947)	9	7	Aged: at home	1409	1034	2313	369	26·2
	18	7	in almshouses	1434	1079	1877	244	17·0
	12	7	in large institution	1580	1252	1717	129	8·2
Bransby, Daubney & King (1948–9*b*)	18	3	(By calculation)	1908	1360	2843	352	18·4
			(By analysis)	1854	950	2506	395	21·3
Kitchin, Passmore, Pyke & Warnock (1949)	71	7	Students: at home	2180	1450	3160	370	17·0
	74	7	in lodgings	2280	1520	3220	400	17·5
	26	7	in hostel	2330	1750	3080	310	13·3
Yudkin (1951)	6	28	Students	2157	1100	2750	—	11·0
Bransby & Osborne (1953)	178	7	Elderly	1746	< 1000	> 3000	427	24·5
Booyens & McCance (1957)	2	7–14	Scientific workers	2007	1063	2471	—	—
Durnin, Blake & Brockway (1957)	12	7	Housewives	2100	1593	2435	245	11·7
	12	7	Their daughters	2220	1777	2720	333	15·0
Cook & Wilson (1960, private communication)	205	7	Students	2429	—	—	462	19·0
Durnin, Blake, Brockway & Drury (1961)	17	7	Elderly, living alone	1894	1107	2283	299	15·8
Durnin, Blake, Allan, Shaw & Blair (1961)	21	7	Elderly, at home	1944	1243	2886	404	20·8
Copping (1962, unpublished)	82	7	Students	2157	1340	4014	464	21·5
			Pregnant women					
McCance, Widdowson & Verdon-Roe (1938)	120	7	Various	2347	1163	3522	497	21·2
Roscoe & McKay (1946)	35	7		2550	1660	3650	473	18·5
Hobson (1948)	111	7		2400	1600	3500	430	18·0
Thomson (1958)	101	7	Social class: I and II	2633	—	—	482	18·3
	109	7	III	2521	—	—	487	19·3
	279	7	IV and V	2354	—	—	513	21·8
Thomson (1958, unpublished)	489	7	All the above classes	2449	1126	4152	503	20·5

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Table 4. *Variations in energy intake: children and adolescents*

Source	No. of subjects	Period of survey (days)	Sex	Age (years)	Mean daily value for all subjects (kcal)	Minimum daily mean for any subject over the period (kcal)	Maximum daily mean for any subject over the period (kcal)	Standard deviation of subject means (kcal)	Coefficient of variation of subject means (%)
Cook, Davidson, Keay & McIntosh (1944)	39	7	♂	14–15	2191	1313	4027	482	22·0
Fowke (1945)	24	14		14–17	3097	2078	4185	446	14·4
Widdowson (1947)	20	7		1–2	1154	811	1547	210	18·2
	23	7		2–3	1406	959	1929	241	17·1
	20	7		3–4	1691	1250	2340	316	18·7
	23	7		4–5	1939	1210	2574	362	19·6
	28	7		5–6	1732	1312	2144	226	13·1
	24	7		6–7	1940	1152	2528	340	17·5
	21	7		7–8	2178	1644	2827	309	14·1
	23	7		8–9	2170	1597	3113	345	15·9
	21	7		9–10	2443	1823	2941	257	10·6
	25	7		10–11	2501	1596	3533	427	17·0
	27	7		11–12	2521	1972	3246	373	14·8
	22	7		12–13	2630	2063	3532	434	16·5
	21	7		13–14	2756	2150	3611	400	14·5
	36	7		14–15	3065	1840	4121	546	17·8
	22	7		15–16	3440	2457	5395	646	18·8
	27	7		16–17	3105	1363	4341	636	20·5
	32	7		17–18	3223	1754	4528	478	14·8
	20	7		18–19	3427	2338	5221	703	20·4
	23	7	♀	1–2	1152	842	1631	207	18·0
	21	7		2–3	1431	1055	2048	252	17·6
	21	7		3–4	1533	991	2328	294	19·2
	20	7		4–5	1718	1085	2263	318	18·5
	20	7		5–6	1708	1300	2288	298	17·5
	25	7		6–7	1985	1517	2543	279	14·0
	22	7		7–8	1995	1524	2708	283	14·2
	20	7		8–9	2086	1482	2971	336	16·1
	20	7		9–10	2165	1589	2802	297	13·7
	27	7		10–11	2345	1649	3180	376	16·0
	30	7		11–12	2292	1585	3725	446	19·5
	31	7		12–13	2370	1804	3481	438	18·5
	34	7		13–14	2504	1706	3736	452	18·1
	38	7		14–15	2637	1901	3617	451	17·1
	41	7		15–16	2588	1539	3550	504	19·4
	36	7		16–17	2363	1718	3142	389	16·5
	31	7		17–18	2513	1620	3318	372	14·8
	21	7		18–19	2513	1876	3452	376	15·0
Bransby, Daubney & King (1948–9a)	49	3	♂ and ♀	10–14	2660	By weighing		507	19·1
					2771	Using homely measures		423	15·3
					2607	By questionnaire		487	18·7
					2381	By chemical analysis		218	9·2
Ministry of Food (1948, unpublished)	6	7	♂ Adolescent		3044	2507	3717	484	15·9
	9	7	♀ Adolescent		2565	2194	2807	264	10·3
Roscoe & McKay (1946)	52	7	♂ and ♀	7–12	2695	1730	3700	437	16·5
Bransby & Fothergill (1954)	461	7	♂ and ♀	6–12 months	1080	—	—	290*	26·9
				1 year	1330	—	—	430	32·3
				2	1540	—	—	410	26·6
				3	1590	—	—	380	23·9
				4	1730	—	—	370	21·4

*'Excludes two children with an abnormally high intake'.

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relatively free choice, at least in quantity, of food. Studies on subjects consuming experimental diets have been excluded (e.g. that of Passmore, Thomson & Warnock, 1952). A few studies were included which did not meet these criteria, but appeared to yield reliable results.

All the estimates of variation given in Tables 2, 3 and 4 were calculated from the subjects' mean daily intakes over the period of the survey, usually a week. If the length of the survey exceeded 1 week, e.g. those of Yudkin (1951), Edholm *et al.* (1955) and A. M. Copping (1961, private communication), mean values for each week were available and were used, although it meant taking more than one weekly mean for some individuals, thus introducing an element of temporal fluctuation, which would tend to decrease the estimate of variation. In nearly all studies which did not include measurement of energy expenditure, the daily intake was calculated from the week's total consumption of individual foods and thus the only standard deviation that could be calculated was that based on the subjects' weekly means.

It is arguable whether the mean daily intakes obtained from a week's survey are adequate for our purpose. Yudkin (1951) reported that mean weekly values for the same individual in a dietary survey on female students can differ by as much as 68%. On the other hand, in a study of the diets of bank officials, Marr, Heady & Morris (1959) and Heady (1961) advanced evidence of the stability in repeat surveys of weekly averages for the same individuals. Thomson (1958) obtained similar evidence for pregnant women. The only long-term dietary survey known to us was done by Chappell (1955), who reported results for one woman for 70 weeks and for one man for 13 weeks. We have not included these observations, because their standard deviations would reflect fluctuations in the consumption of two individuals over time. However unsatisfactory a solitary week may be in representing energy intake (or expenditure), we are forced to accept it. Were we to confine our attention to estimates based on a longer time our study could not have been made.

Two important influences on the magnitude of the variation between individuals are reflected in Tables 2, 3 and 4. One is the wartime and postwar rationing of food. Though rationing did not necessarily reduce calorie intake, it may have reduced the extent to which people varied their intake. Thus, all investigations made when food supplies were controlled may provide rather lower estimates of variation than the true values. The second influence is that of institutional life which also might be expected to reduce individual variation. This effect can be seen in the results of Kitchin, Passmore, Pyke & Warnock (1949) who compared the diets of students living at home, in lodgings and in hostels, and in those of Pyke, Harrison, Holmes & Chamberlain (1947) for elderly persons living in institutions, almshouses and at home. The estimates of variation obtained from the results of Edholm *et al.* (1955) and Adam *et al.* (1957, 1958, 1959) are also likely to be low because, as we have stated already, their groups were fairly homogeneous and also because servicemen may not vary as much in their food intake as other people. Indeed one phase (phase II) of the Adam *et al.* (1957) survey was deliberately excluded from our calculations because in it all subjects received precisely the same food: in other phases they could obtain supplementary foods, so that there was possibility of greater variation.

The group giving the highest standard deviation (Widdowson, 1936) was probably one of the most heterogeneous, and thus differences in age, body-weight and activity must have played a considerable part in inflating this particular estimate. However, high standard deviations were also found by Kitchin *et al.* (1949) for students living at home and by Bransby (1954) for industrial workers. The results of Booyens & McCance (1957) probably give an abnormally high estimate because, as with the corresponding measurements of expenditure, their studies were for four men selected because of their extreme basal metabolic rates.

The influence of age on variation in energy intake may be assessed by comparing Table 4 with Tables 2 and 3, and by comparing results for younger and older groups of adults. The young seem to vary between themselves as much as the old.

Variations in a homogeneous group

The groups studied by Adam *et al.* (1958, 1959) were army recruits of fairly uniform age engaged in similar activities. They were not all of the same body-weight. Although the use by the Second Committee on Calorie Requirements of the Food and Agriculture Organization (FAO: Second Committee on Calorie Requirements, 1957) of a formula to allow for the relationship between body-weight and energy expenditure has been criticized (Thomson, Billewicz & Passmore, 1961) on the grounds that increasing weight appears to be associated with diminishing physical activity rather than increased appetite, we used the FAO formula in an attempt to distinguish the variation due to differences in body-weight in one of the fairly homogeneous age–sex–occupation groups studied by Adam *et al.* (1958). Whereas the coefficient of variation on expenditure observed was 11·8% (see Table 1), that which might be expected from differences in body-weight was found to be 6·0% leaving an unexplained variation of 10·2%.

We also selected the study of Adam *et al.* (1958) in an attempt to eliminate the effects on energy intake of age, sex, climate and activity and to determine the remaining variation after making allowance for differences in body-weight. The coefficient of variation shown in Table 2 for this group is 16·4%; that which might be expected from differences in body-weight was calculated to be 6·4% leaving an unexplained variation of 15·1%.

There is no ready explanation of the rest of the variation in either expenditure or intake, though there is a clue worth pursuing in the interesting observation of Rose & Williams (1961) that, if walking at their natural speeds, their group of 'large eaters' all walked faster than any of their 'small eaters'. Similar differences were observed in the speeds of going up and down stairs. These workers found no evidence that a man's speed of walking affects the amount of energy spent in covering a given distance, a result in accord with those of Passmore & Durnin (1955), but as they pointed out the faster a person moves the more time there is left over 'to use up in other pursuits'.

Table 5. *Frequency distributions of energy intake and expenditure (adults)*

No. of individuals (mean for 7 days)

kcal/day	Intake: A. M. Copping (1961, unpublished) Females	Intake: Bransby & Osborne (1953) Females	Intake: A. M. Thomson (1958, unpublished) Females, pregnant	Intake: Adam, Best, Edholm, Fletcher, Lewis & Woolf (1958) Males	Intake: Ministry of Food (1949, unpublished) Males	Intake: Bransby & Osborne (1953) Males	Intake: Heady (1961) Males	Expenditure: Adam, Best, Edholm, Fletcher, Lewis & Woolf (1958) Males
Less than 1000	—	4	—	—	—	2	—	—
1000	—	46	11	—	—	10	—	—
1250	5			—	—		—	—
1500	12	80	25	—	—	39	1	—
1750	36		47	—	—		2	—
2000	39	43	97	3	1	50	6	—
2250	23		101	2	1		14	—
2500	7	4	91	5	5	19	24	—
2750	3		48	6	12		28	4
3000	5	1	36	11	10	5	24	10
3250	1		18	19	13		12	12
3500	1	—	15	26	13	—	4	13
3750	1	—		31	7	—	2	20
4000	1	—	—	27	8	—	1	16
4250	—	—	—	20	4	—	—	8
4500	—	—	—	10	—	—	—	2
4750	—	—	—	3	—	—	—	2
5000	—	—	—	4	—	—	—	—
5250–5500	—	—	—	2	—	—	—	—
Total frequency	134	178	489	169	74	125	118	87

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Comparison of variations in energy expenditure and intake

Variations in Table 1 of expenditure are generally smaller than those in Tables 2, 3 and 4 of intake. This difference may be more apparent than real because the methods used for measuring expenditure, being more directly physiological, may be more accurate. However, there may be reasons why energy expenditure is, in fact, less variable (between individuals of the same age and sex) than energy intake. If so, the use of intake data to estimate requirements is justifiable for mean values, but not for estimates of variation.

Form of the variation for adults

Many workers when faced with the problem of the shape of the distribution about the mean have assumed it to be normal. Woolf (1954), however, suggested that 'the incomplete gamma function distribution . . . fits the data fairly well' and gave examples to show how much this affected estimates of undernutrition.

One set of data for energy expenditure (Adam *et al.* 1958) and seven for energy intake (A. M. Copping, 1961 (private communication); Bransby & Osborne, 1953 (males and females separately); Thomson, 1958; Adam *et al.* 1958; Ministry of Food, 1949 (unpublished records); Heady, 1961) provided sufficient results to study the normality of their distributions, which are given in Table 5. This study showed (Harries, Hobson & Hollingsworth, 1961) that only for the observations of Copping (1961, private communication) was the distribution non-normal, though some departure from normality was evident in the data of Thomson (1958). This meant that a normal curve would give a fairly good fit to the other six distributions, some of them being remarkably symmetrical.

If the extreme values in Tables 1, 2, 3 and 4 are expressed as distances from the mean in units of the standard deviation, it is confirmed (Harries *et al.* 1961) that energy expenditure is symmetrical, but energy intake may be slightly non-normal at the lower extreme values: the minima are slightly higher than one would expect on grounds of strict normality. This is not, however, sufficiently serious to warrant the use of any distribution other than the normal. Care has been taken in interpreting minimum values of energy intake, since slight illnesses of the subjects can lead to unrealistic results. Low results due to indisposition have, as far as possible, been excluded from these calculations, either by us or by the original authors.

Conclusions

Widdowson (1947) in her study of the diets of children discussed the 'enormous differences between individuals' that she found in calorie intake in relation to sex, age, body-weight, height and body surface area and showed that after all these factors had been taken into account, large variations still existed from one child to another. She considered other possible explanations of individual variation and concluded that 'much more research lies ahead before we can begin to understand why one person can live on half the calories of another . . . '.

We have reviewed results more recently obtained, particularly on adults, both for expenditure and intake, and have reached the same conclusion. When all known causes of variation are taken into account, large unexplained differences between individuals remain, though it would seem that these are less for expenditure than for intake.

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Genetic variation in the nutrition of *Drosophila melanogaster*—some general inferences

By Forbes W. Robertson, *Agricultural Research Council Unit of Animal Genetics, Institute of Animal Genetics, Edinburgh*

Introduction

To consider genetic variation in the nutritional requirements of *Drosophila melanogaster* at a symposium where most of the interest centres on man would seem to call for some justification. The physiology and development of fly and mammal might appear sufficiently different to limit the usefulness of comparisons between them. With respect to quantitative requirements for specific nutrients this may be quite true, but is less relevant when we consider the more general problem of genetic variation in relation to diet. By virtue of the Mendelian basis of genetic variation, data culled from any population of diploids add to the common store of concepts and models which is drawn upon whenever we try to interpret variation between individuals of any species, including man. Variation within and between populations is discussed in terms of breeding structure, population size, inbreeding, fluctuations in selection pressure, mutation, gene flow between populations and the significance of deviations from the mean, for survival and reproduction, in different traits.

During the last 15 years or so experimental work with *Drosophila*, the mouse, the hen and other species has established an organized approach to polygenic variation and to methods for describing its properties. Because of differences in life cycle, some species are better suited than others for tackling certain problems and, of course, in *Drosophila* the genetic analysis can be taken furthest. The genetic behaviour of similar traits in these widely differing species has much in common, judged by the effects of selection and inbreeding. This is especially true of characters such as body size, growth rate and survival that play corresponding roles in the general economy. There is therefore sound reason for looking at evidence for genetic variation in the nutritional requirements of *Drosophila* for clues to what we might, or should, look for in man.

I shall describe some of the results of experiments I have carried out during the last 2 or 3 years, some already published (Robertson, 1960*a*,*b*,*c*; Prabhu & Robertson, 1961), others in preparation, illustrating only the general features. These experiments were not designed to study genetic variation in nutritional requirements in quite the same way as is commonly understood in the field of nutrition. They arose as part of a general study of the properties of genetic variation, which influences body