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## Fat Combustion and Metabolic Rate of Flying Locusts (*Schistocerca gregaria* Forskal)

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# FAT COMBUSTION AND METABOLIC RATE OF FLYING LOCUSTS (*SCHISTOCERCA GREGARIA* FORSKÅL)

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The nature and the amount of fuel used by flying *Schistocerca gregaria* Forskål have been estimated from direct analyses of the total content of fat and glycogen in control groups and in the corresponding flying groups, i.e. groups which had flown continuously for several hours. The locusts were cage-bred and resembled phase *gregaria* or phase *transiens*. Each batch was so homogeneous that it was possible to select two groups, consisting of six to fifteen individuals, which did not differ by more than 2% from one another. Because of this uniformity and because of the high rate of metabolism during flight, this rate could be estimated within about  $\pm 15\%$  (in one case  $\pm 30\%$ ).

For flight, the locusts were suspended at the periphery of a special roundabout (Krogh & Weis-Fogh 1952). The groups could choose the flying speed that they would naturally adopt. The speeds and durations of flight were of the same order of magnitude as observed in swarms in nature, so that some of the results could be applied to natural swarms.

Analyses of the geometric similarity and of the distribution and nature of dry matter made possible an estimation of average size and gross composition of fully developed but sexually immature *S. gregaria*. Such standard individuals were found to contain large amounts of lipids (an average of 10% of the fresh weight), and about 85% of the stored energy was in the depot fat. The cuticle and the wing muscles of newly emerged adults (fledglings) contained only one-third of the dry matter that was found in fully developed individuals, and the accumulation of dry matter lasted 2 or 3 weeks. Fledglings were unable to fly or disinclined to fly for long.

In spite of differences in age, sex, training and food, in all flight experiments fat constituted the principal source of energy, the remainder being glycogen. An average of 80 to 85% of the total energy expenditure was derived from fats or fatty acids during the first 5 h of flight. All the

available glycogen was utilized during the first few hours, most of it probably within the first hour. Flight was nevertheless maintained for several hours without reduction of speed.

The metabolic rate on the roundabout increased approximately with the second power of the flying speed. The speed was almost independent of temperature and varied between 2.3 and 3.7 m/s, but the speeds recorded from a large number of experiments were equally distributed around 3 m/s; the average metabolic rate of flying *Schistocerca* was about 75 kcal/kg/h. This corresponded to an oxygen uptake of 16 l. O<sub>2</sub>/kg/h. The values deduced for the first few minutes after the start were three times higher, and cruising rates twice as high were sometimes maintained for several hours. An average flight performance of 5 h at 3 m/s required twice as much energy as was contained in the constituent proteins of the wing muscles. Sustained flight therefore depends on large-scale transport of fuel from the stores to the muscles. The fat body delivered 85 to 90 % of the energy, and the remainder was mobilized from wing muscles, legs and wings. Since even the remote cells of the wings provided stores of fuel, the mobilization was of a general nature and the transport of fuel took place via the blood.

Concerning migrating swarms the following was suggested: in the morning, milling and surging of groups of locusts before mass departure tends to empty the stores of glycogen; the proper migratory flight therefore takes place at the expense of fat and, under suitable climatic conditions, the endurance of flight is proportional to the amount of fat in storage before the start. Standard individuals with 10 % of fat (by fresh weight) should be able to fly continuously for about 12 h, 20 h being the upper limit (15 to 16 % of fat). The amount of vegetation daily consumed by a migrating swarm probably weighs as much, and possibly three times as much, as the weight of the swarm. Sufficient time and opportunity for feeding will therefore be essential for migrations. A large migrating swarm (say 15000 tons) was estimated to require as many calories per day as do 1.5 million men.

The rate at which the wing muscles of locusts converted energy was between 400 and 800 kcal/kg muscle/h; i.e. the same rates as found in hovering humming birds and flying *Drosophila*. Even for very intense muscular work, fat cannot therefore be regarded as inferior fuel in well-oxygenated muscles. An increasing amount of evidence from the literature favours the view that fat can be utilized directly. A possible cause for the lowered mechanical efficiency of man when fat is oxidized is the formation of ketone bodies parallel to the direct combustion of fat. On the other hand, initial mobilization seems to be slower for fat than for glycogen. When flight starts, this gives glycogen an advantage over fat, whereas the weight economy, and thus the endurance, is decisively improved by the ability to utilize stored fat; this will be further discussed elsewhere.

## 1. INTRODUCTION

The metabolic rate of resting animals need not bear any constant relation to the rate reached during activity, except perhaps in homoiothermal vertebrates, in which the readiness for activity is continuously maintained at the expense of high resting rate. Resting insects, for example, convert energy at moderate rates compared with birds and small mammals (Zeuthen 1947), but during flight their metabolic rate is increased twenty to a hundred times and reaches the highest values hitherto measured (Jongbloed & Wiersma 1935; Davis & Fraenkel 1940; Zeuthen 1941). From the point of view of the survival of a terrestrial animal, the metabolism during activity is at least as important as the metabolism during rest, the daily amount of muscular work often requiring much more energy than is used for maintenance. Most investigators of heavy muscular work have confined their studies to mammals. Yet, in some respects, flying insects are more suitable objects for experiments, because combustion in the wing muscles by far exceeds the combustion in the remaining tissues, facilitating the interpretation of the results. Moreover, the wing system of insects represents the climax of animal evolution both in frequency of movement (Sotavalta 1947) and in continuity of high power output.

In flying bees, blowflies, and butterflies, the oxygen uptake can reach 100 l. O<sub>2</sub>/kg body weight/h (see references above). In *Drosophila* (Chadwick & Gilmour 1940) and desert locusts (Krogh & Weis-Fogh 1951) the figures range about 20 l. O<sub>2</sub>/kg/h. While bees and flies exclusively utilize carbohydrates for flight (Jongbloed & Wiersma 1935; Beutler 1937; Chadwick & Gilmour 1940; Williams, Barness & Sawyer 1943; Chadwick 1947; Wigglesworth 1949), measurements of the respiratory exchange of desert locusts revealed that the respiratory quotient (R.Q.) decreased from 0.82 to 0.75 during the first 30 to 90 min of tethered 'flight' (Krogh & Weis-Fogh 1951). Carbohydrate could not therefore be the only source of energy; the contribution made by fat seemed to increase as flight went on. In view of the high concentration of amino-acids in insect blood it was also possible that protein provided some of the energy. Since the 'flying' took place in a small respiration chamber, it seemed possible that the metabolic rate was lower than in free flight. Finally, fat is generally considered an inferior source of energy for intense muscular exercise. As far as insects are concerned, Wigglesworth (1949) suggested that the low speed of combustion of fat prevented this material from being used in those insects that need a high-power output for moving their wings. *Drosophila*, for example, used stored fat when resting and running, but the wing muscles were unable to make use of anything but carbohydrates.

The purpose of my work has been to study the metabolism of desert locusts when performing prolonged flight, especially: (1) the nature of the fuels used; (2) the metabolic rate and its relation to the flying speed; (3) the storage of fuel and the endurance of flight. In addition, some problems relating to the uniformity of the experimental material, to the development of the ability to fly, and to the mobilization of fuels have been investigated.

## 2. METHODS AND MATERIAL

### (a) General procedure

Each batch of desert locusts (*Schistocerca gregaria* Forskål) was divided into two groups, care being taken to make the groups as similar as possible. At the beginning of the experiment the one group, i.e. the controls, was killed, and then weighed before and after drying. The other group was treated similarly after it had flown for a number of hours on a specially constructed roundabout (Krogh & Weis-Fogh 1952). Both groups were analyzed for fat or, in two experiments, for glycogen. The consumption of fuel should equal the differences found between the groups, if they were similar before the experiment and if the faeces given off were accounted for. Metabolic rates are seldom estimated from direct determinations of the utilization of fuel because methods for measuring the oxygen uptake are much more sensitive. It is difficult, however, to measure the oxygen consumption of insects flying under tolerable aerodynamic conditions and, since the amount of fuel combusted was known to be large, a direct estimate turned out to be possible.

It was essential that the control group and the flying group should be similar. But the size, the bodily proportions, and the chemical composition of locusts vary with phase, age and treatment. For this reason the selection of groups required special precautions, and an investigation of the degree of similarity of the experimental material was necessary. Since the results will also be used in other connexions, they are given in some detail.

(b) *Material*

*Breeding and treatment.* The locusts were bred in crowded cages at the Anti-Locust Research Centre, London. The coloration (see table 1) was nearest to that of phase *gregaria*, but the biometry corresponded to phase *transiens* (see table 2). They were sent by air mail to Copenhagen 5 to 7 days after the final moult. Males and females were kept in separate cages, at thirty to forty individuals per cage. During daytime, i.e. from 9 a.m. to 10 p.m., each cage (60 × 60 × 40 cm) was heated by a 40 W bulb, and the locusts could bask on

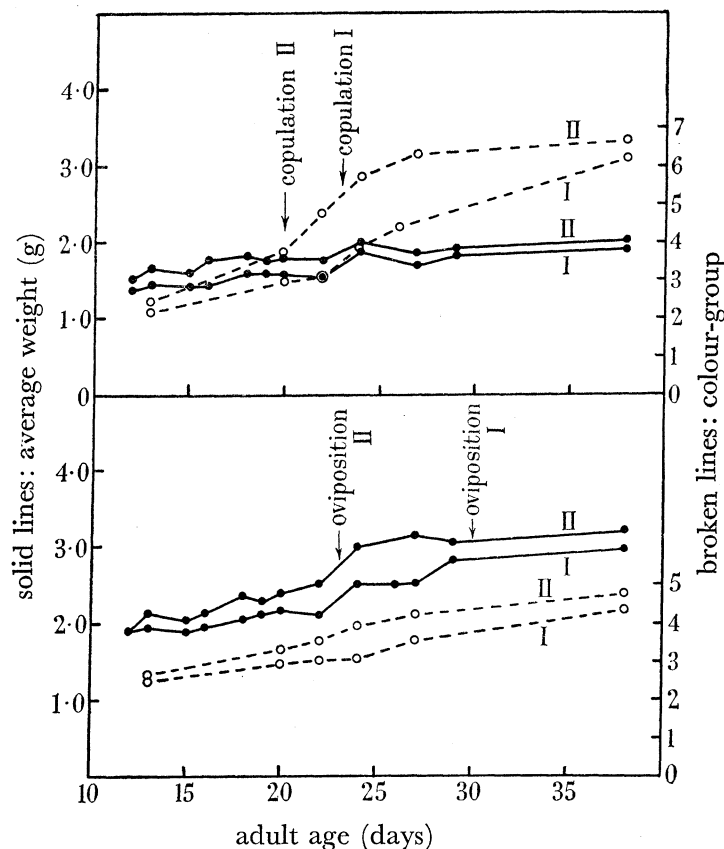


FIGURE 1. Effect of diet upon weight, colour-group and sexual maturation of cage-bred *Schistocerca gregaria* (males above, females below). Group I was given fresh grass + hay, and group II was given fresh kale + hay. The locusts became sexually active at the transition between colour-groups 3 and 4.

the floor and the walls. The body temperatures of the basking locusts were estimated by mounting thermistors within dried and wax-filled insects and placing them in various positions in the 'sun'. Most of the day they ranged between 30 and 35° C. During the night a cold-water installation on the ceiling of the cage caused the body temperature to fall to 13 to 14° C. The locusts were thus exposed to temperature changes resembling the daily régime in nature. The humidity of the air was not controlled, it being considered of minor importance when the animals had continuous access to abundant fresh leaves. Before an experiment the locusts were allowed to bask for at least 1 h.

During the summer the food consisted of fresh leaves of cocksfoot (*Dactylis glomerata*); but in winter the animals were given green kale (*Brassica oleracea*), which was readily

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eaten. Besides kale, dried grass was always offered, for otherwise the locusts developed diarrhoea. They thrive on both diets as illustrated in figure 1. It shows the changes in average weight (full lines) and colour-group (broken lines) of adults from the same batch (no. 17), which was divided into two groups of thirty individuals each. Apart from the food, they were kept under identical conditions. Group I received fresh grass and hay and group II fresh kale and hay. The first copulations and ovipositions were noted. The kale-fed animals advanced more rapidly than the grass-fed, but both groups became mature and produced eggs. It was therefore concluded that both kinds of food contained sufficient nutrients.

TABLE 1. COLOUR-GROUPS OF CAGE-BRED *SCHISTOCERCA GREGARIA*

development	base of hind wings	colour-group	main colour patterns*	
immature	without colour	1	(a) pinkish (b) light brown (c) pink and bluish	
		2	(a) pinkish (b) brown (c) pink and brown	
		3	(a) brownish with purple or greyish legs (b) brown (c) brown	
	mature	with yellow tinge	4	like group 3
			5	(a) intermediate (b) with yellow patches (c) brown
			6†	(a) yellowish (b) yellow (c) brown
			7†	(a) yellow (b) yellow (c) yellow

\* (a) General appearance.  
(b) Abdomen.  
(c) Pterothorax.

† Males only.

Upon arrival from London the locusts were soft and pinkish, gradually getting harder and more brownish. The bases of the hind wings were colourless. If the animals were kept at ordinary room temperature, sexual development was arrested, the brownish appearance remained in both sexes, and the wings remained colourless. In the heated cages, however, a yellow tinge at the base of the hind wing appeared 18 to 25 days after emergence, the coloration of the other parts of the body being still unchanged. This yellowing of the wing membrane coincided with the onset of sexual maturation and served as a sensitive indicator of whether the animals had matured or not. Thus males which had no yellow were not seen to copulate, and the deposition of egg materials in the females did not start until the yellow colour became visible (cf. figures 1 and 2). When selecting the groups, the individuals should be in the same physiological state and their weight and colour were therefore noted at regular intervals, the seven colour-groups in table 1 being distinguished. Whereas the colour of the males changed considerably with age, the weight, on the other hand, remained remarkably constant from the time when they reached colour-group 3 until senescence. In females, however, the formation of eggs caused a sudden increase of weight at the transition between colour-groups 3 and 4. Forty individuals from batch

no. 15 were followed daily from the last moult and during the next 2 months. Figure 2 shows a characteristic result. The constancy of the weight of the male strongly contrasts with the rapid and large fluctuations seen in the female after it had passed colour-group 3. The weight of egg-producing females often increased 30 to 40 %, and a single mature female might therefore cause considerable experimental error in a material otherwise consisting of immature animals. Furthermore, mature females turned out to be poor fliers. On the other hand, young locusts of colour-group 1 and 2 were soft, not full grown (cf. figure 5), and weak fliers as well. Females therefore had to be of colour-group 3 for flight experiments, but full grown males could be used whether immature or mature.

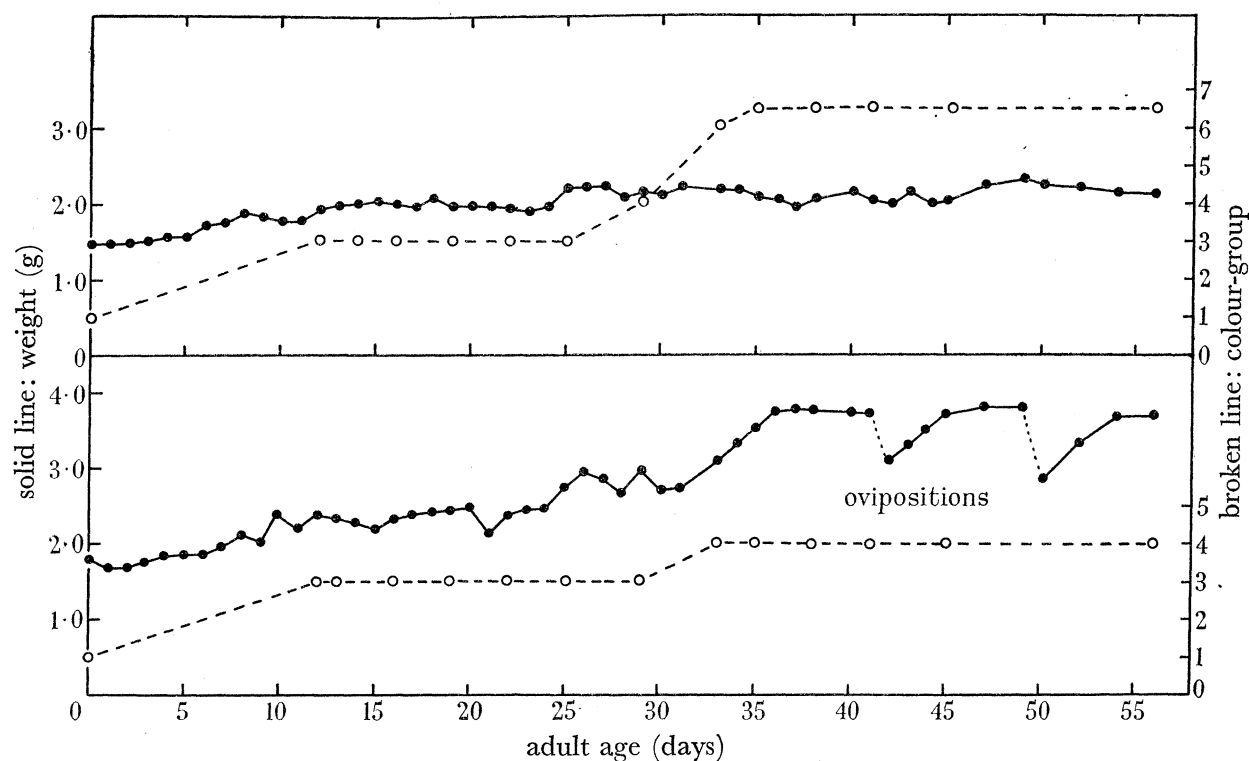


FIGURE 2. Typical changes in weight and colour of a male (above) and a female (below) *Schistocerca gregaria*. The deposition of egg materials started at the transition between colour-groups 3 and 4. The sudden decreases in weight of the female at the 42nd and 50th day corresponded to ovipositions.

Immature migrating desert locusts from nature are described as pinkish (cf. Gunn, Perry, Seymour, Telford, Wright & Yeo 1948). Since young adults as well as mating and egg-laying migrants fly less vigorously than full-grown but sexually inactive locusts (Kennedy 1951), it is probable that the cage-bred animals of colour-group 3 can be compared with 'full migrants'.

Each locust was numbered by means of cellulose paint so that its history could be followed. In order to prevent the locusts from damaging their wings by jumping in the cages, the metatibiae and the mesotarsi were cut off and the wounds covered with wax; this also helped in reducing the amount of trancy (Krogh & Weis-Fogh 1952). During the operation the animals were narcotized in a 1:2 mixture of carbon dioxide and atmospheric air, the exposure lasting from 30 to 60 s. The gases were mixed by means of the

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simple apparatus shown in figure 3. It works on the suction-pump principle, air being sucked through the bored plug in a proportion which turned out to be nearly independent of the carbon dioxide pressure; the composition could therefore be altered by changing the bore of the plug only. The locusts were not subjected to oxygen lack. Ribbands (1950) suggested that the detrimental effects found in bees after carbon dioxide narcosis were caused by oxygen lack. In order to make sure that the narcosis and the operation did not injure *Schistocerca gregaria*, a young batch (no. 14, colour-group 2.5) was divided into three groups. The first group was narcotized and operated in the usual way, the second was only operated, and the third remained untreated. The animals were placed together in the same cage and the weight and the colour were followed during the next 3 weeks, i.e. until 10 to 12 days after they became mature. During this period it was impossible to demonstrate any differences in weight and colour between the three groups. Many additional experiments with single animals subjected to narcosis for much longer periods failed to show any detrimental effect on the ability to fly. It was therefore concluded that neither the narcosis nor the operation affected the experimental animals significantly.

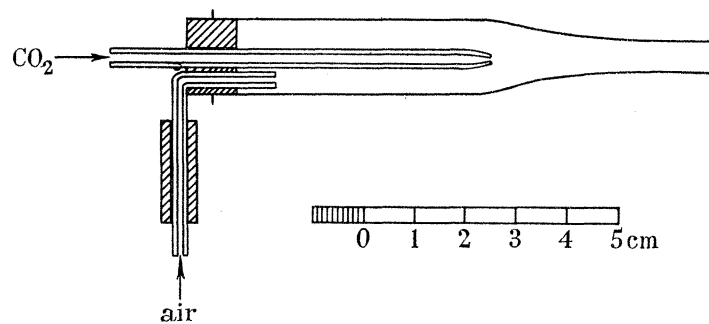


FIGURE 3. Simple narcotizer used for mixing carbon dioxide and air in known proportions.

*Similarity and selection.* A batch numbered at most eighty individuals. But since males and females were treated separately and some locusts could not be used because they were disinclined to fly or matured abnormally, each group seldom numbered more than twelve individuals. The considerable variation in size and weight of the individuals therefore hampered the selection of two similar groups. Now the integument of adult insects retains its size and shape and, apart from the abdomen, the remaining parts do not change their linear dimensions or volume. Provided that the locusts were geometrically similar, the weight ratio between two groups which did not differ physiologically, i.e. were equally aged, developed, hydrated, loaded with fuels, etc., should equal the ratio between their volumes.

The biometry of locusts is known to vary with pre-adult conditions of life (Uvarov 1928; Faure 1932). In phase *solitaria* desert locusts, the ratio between the length of the forewing,  $E$ , and the hind femur,  $F$ , averages 2.06 in both sexes, whereas in typical migrating *gregaria* swarms the average  $E/F$  ratio can be as high as 2.25 in males and 2.30 in females (information from Dr P. B. Uvarov). Table 2 shows that the batches used for experiments had intermediate ratios that did not vary much. The standard deviation from the mean of a batch ranged from 0.04 to 0.07.



TABLE 2.  $E/F$  RATIOS OF ELEVEN BATCHES OF CAGE-BRED *SCHISTOCERCA GREGARIA*

batch no.	5	6	7	8	12	13	14	15	16	17 <sub>a</sub>	17 <sub>b</sub>
males	2.16	2.15	2.17	2.15	2.16	2.13	2.13	2.15	2.15	2.15	2.14
		no. of individuals			216	average ratio			2.15 ± 0.003		
females	2.17	2.15	2.14	2.16	2.19	2.17	2.17	2.17	2.16	2.18	2.17
		no. of individuals			206	average ratio			2.17 ± 0.004		

The batches were therefore comparable, and the size of an individual could be expressed in terms of  $E$  and  $F$  provided that these quantities were representative of the body as a whole. In fifteen females (average  $E/F = 2.14$ ; s.d. = 0.05) three thoracic lengths were measured with an error less than  $\pm 0.5\%$ . The relative length of each individual was calculated by dividing its length index by the average index of the group, the length index being the fifth root of the product of  $E$ ,  $F$ , and the above three quantities. If the experimental animals were geometrically similar, the wing length of an individual, for example, divided by its relative length should equal the average wing length of the group. When calculated for the different quantities the standard deviations from the mean amounted to 1.5% as far as the thorax and the femur were concerned, and to 2.2% when the forewings were considered. These figures express to what degree the locusts were geometrically similar. Let  $l = (E \times F)^{\frac{1}{5}}$ ,  $s = E \times F$ , and  $v = (E \times F)^{\frac{3}{5}}$  be indices of length, surface area and volume respectively. These indices would then represent lengths, areas and volumes, the standard deviations from the true mean being about 2, 4 and 6%. This was checked by estimating the areas of the mesoscutum and the metascutum in sixteen locusts and the wing areas in thirty other locusts by weighing photographic projections. The standard deviation did not exceed 4% in any case, and the mean indices of a group consisting of ten to fifteen individuals would therefore represent lengths, areas and volumes with a standard error of less than  $\pm 1$ ,  $\pm 1.5$  and  $\pm 2\%$  respectively. The two groups were selected so that the ratio between their weights did not deviate more than 2% from the ratio between the sums of the volume indices. Furthermore, the size grouping of the individuals was made equal. The initial composition of the flying group could therefore be estimated from the analyses of the controls, the error being determined by the variation ascertained within the latter (cf. p. 11).

*Standard types.* The average indices found in ten batches are seen in table 3,  $E$  and  $F$  being measured in centimetres. The average volumes varied considerably (cf. batches 5 and 12), but the ratios between the volume indices of females and males ( $v_{\text{♀}}/v_{\text{♂}}$ ) were nearly constant and averaged 1.34, the s.d. being only 0.03. The corresponding ratio between surface indices was 1.22, and in the actual measurements of wing and scutum areas the ratios found did not differ more than 1 to 2% from that figure. It was therefore concluded that the different series were comparable in spite of large variations in size. Furthermore, males and females could be considered similarly shaped with respect to thorax, legs and wings. i.e. to the locomotory systems.

The geometric similarity of males and females suggested that immature locusts might also be similar in other respects. Table 4 shows the average weight of males and females before and after sexual maturation, each value being the mean of three to seven weighings. In immature locusts the ratio of weight of female to male averaged  $1.36 \pm 0.02$  and thus

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TABLE 3. AVERAGE INDICES OF LENGTH ( $l$ ), SURFACE ( $s$ ) AND VOLUME ( $v$ ) OF CAGE-BRED *SCHISTOCERCA GREGARIA*

batch no.	length = $(E \times F)^{\frac{1}{2}}$		surface = $E \times F$		volume = $(E \times F)^{\frac{3}{2}}$		$v\text{♀}/v\text{♂}$
	♂	♀	♂	♀	♂	♀	
5	3.45	3.82	11.9	14.6	41.2	55.8	1.35
6	3.62	3.96	13.0	15.7	47.5	62.0	1.31
7	3.60	3.95	12.9	15.4	46.5	61.5	1.32
12	3.73	4.09	13.9	16.6	51.7	68.9	1.33
13	3.58	3.97	12.8	15.8	45.9	62.6	1.36
14	3.59	3.98	12.9	15.8	46.4	62.8	1.35
15	3.55	3.91	12.6	15.3	44.8	59.8	1.34
16	3.63	4.05	13.2	16.3	47.8	65.8	1.38
17a	3.60	3.95	13.0	15.6	46.4	61.7	1.33
17b	3.56	3.88	12.7	15.1	45.1	58.2	1.29
average	3.59	3.97	12.9	15.7	46.3	61.9	1.34

 $E$  and  $F$  were measured in centimetres.TABLE 4. AVERAGE WEIGHT ( $w$ ) OF IMMATURE AND MATURE *SCHISTOCERCA GREGARIA*

batch no.	immature			mature		
	average weight (g)		$w\text{♀}/w\text{♂}$	average weight (g)		$w\text{♀}/w\text{♂}$
♂	♀	♂		♀		
5	1.92	2.52	1.31	1.87	3.22	1.72
6	1.85	2.58	1.39	1.84	3.09	1.68
7	1.62	2.25	1.39	1.84	2.95	1.60
12	1.81	2.50	1.38	1.94	3.29	1.70
13	1.74	2.25	1.29	—	—	—
14	1.85	2.64	1.43	—	—	—
17a	1.54	2.12	1.38	1.89	2.91	1.54
17b	1.76	2.31	1.31	1.97	3.22	1.63
average	1.76	2.40	1.36	1.89	3.11	1.65

TABLE 5. STANDARD DIMENSIONS AND WEIGHT OF CAGE-BRED *SCHISTOCERCA GREGARIA*

Each of the indices has to be multiplied by a dimensionless constant,  $C$ , to give real lengths, areas, and volumes. The constants for wing and scutum areas (p. 8) amounted to

forewings	$C = 0.68$
hindwings	$C = 1.41$
mesoscutum	$C = 0.0166$
metascutum	$C = 0.0165$

*Example.* The total surface area (upper and lower surfaces) of the wings of an average individual amounts to  $2 \times 14.3$  ( $0.68 + 1.41$ )  $\text{cm}^2 = 59.7 \text{ cm}^2$ , i.e. by far the largest part of the exterior surface belongs to the wings, the corresponding area of the remaining parts being estimated to be about  $18 \text{ cm}^2$ .

	index of			
	length = $l$ (cm)	surface = $s$ ( $\text{cm}^2$ )	volume = $v$ ( $\text{cm}^3$ )	weight = $w$ (g)
male (♂)	3.59	12.9	46.3	1.76
female (♀)	3.97	15.7	61.9	2.40
average individual (♂)	3.78	14.3	54.1	2.08

equalled the average ratio between the corresponding volume indices:  $1.33 \pm 0.01$ . Moreover, immature males and females from the same batch did not differ significantly in percentage of dry matter and fat (see table 6, batches 7b and 13). The sexes were therefore practically similar also in gross composition and, in most experiments on flight, only the size and the weight need to be considered. This rendered it reasonable, in most

cases, to refer to a standard *Schistocerca*, i.e. a full-grown sexually immature desert locust of a size, weight, etc., intermediate between average males and average females of colour group 3. The indices and weight of this standard locust are given in table 5, with similar figures for average males and females.

(c) *Special methods*

*Flight.* In the roundabout a number of locusts, sufficient for a statistical treatment, could be made to fly continuously for several hours at their self-chosen average speed. The roundabout was suspended from the ceiling of a small room without windows. During an experiment the temperature and the humidity were kept constant within  $\pm 0.5^\circ \text{C}$  and  $\pm 1 \text{ mm Hg}$  respectively by means of radiators and a simple evaporator. A varnished platform was situated 30 cm below the ring, so that faeces could be collected as soon as they were given off. The flying group was placed in the room at least 15 min before the experiment in order to allow the animals to attain the temperature of the surroundings.

In most cases the animals had had some training. If, during the training, a locust repeatedly refused to fly, it was rejected as a truant.

*Killing and drying.* In experiments 4 to 6 the animals were killed by heating them suddenly to  $70$  to  $80^\circ \text{C}$  in the drying flasks but, in order to prevent vomiting, the remaining animals were killed by means of HCN vapour. The distal parts of the middle and hind legs were cut off, removing the lumps of wax, and the animals were dried in submerged flasks at  $60$  to  $80^\circ \text{C}$ , the flasks being continuously evacuated for 4 to 5 h (water pump). Prolonged drying did not cause any further decrease in weight. The tracheal system of insects fits them for this sort of drying because the transport of water can take place in the gaseous state via the tracheae, even from the most remote parts of the body.

In some experiments the wing muscles and the body cuticle were dried in the same way. Single locusts were heated quickly to  $90^\circ \text{C}$  in a small beaker with moistened cotton-wool. The heating loosened the attachments of the muscles and the hypodermis (cf. boiled shrimps). After bisecting the insect, it was easy to remove the coagulated wing muscles *en bloc*. The cuticle was cleared of any remains of tissue with a strong, thin jet of water.

In experiments 4 to 6 each group was treated as a whole, but in 1 to 3 the insects were weighed individually before and after drying, in order to find the variation within a batch. The variances found in the latter experiments were used, *inter alia*, to estimate the error of the average initial content of dry matter and fat in the earlier experiments.

*Fat.* Besides neutral fats, ethereal extracts normally contain free fatty acids, cholesterol, etc. A diminution in the amount of lipid due to exercise must, however, mainly be caused by combustion of fats and fatty acids. In the grasshopper, *Melanoplus atlantis* Riley, about 75% of the lipids consists of free fatty acids (Giral, Giral & Giral 1946). Timon-David (1930) and Hilditch (1947) pointed out that the unsaturated oleic and linoleic acids made up the largest part and that acids less than  $\text{C}_{18}$  were of no quantitative importance in Orthoptera. Since higher fatty acids and ordinary triglycerides are very alike in physical and energy properties they have been treated together and simply called fats.

The total lipid content of each body was analyzed either immediately after drying (experiments 1 to 3) or after 12 months' storage in bunged drying flasks (experiments 4

to 6); the weight was found to be constant during storage. The fat content varied essentially in the same way in stored and non-stored material, and since only differences in the total amount of lipids were considered, small qualitative alterations in composition would have been of minor importance. For extraction, the body was ground in a mortar together with ignited quartz sand, placed in an extra dense filter cap, and extracted with water-free ethyl ether in a Soxhlet apparatus for 20 h, less than 1 mg being extracted during the next 24 h. The wings and the legs were analyzed *en bloc*. The final drying of the extract took place in nitrogen at 100° C.

*Glycogen.* A locust was decapitated, cut up with scissors, immediately dropped into 4 ml. 60% KOH solution, and placed in a bath of boiling water for 40 to 60 min. Glycogen was analyzed according to von Brand (1936), the resulting glucose being titrated according to Hagedorn, Halstrøm & Jensen (1946). In experiment 7 the animals were treated *in toto*, the faeces given off during flight being incorporated. But in experiment 8 the gut with its content of undigested food was removed and only the remainder analyzed for glycogen. The latter procedure involved disregarding any glycogen which might be in the wall of the alimentary canal (cf. Wigglesworth 1949), but since the average dry weight of the empty gut did not exceed 20 mg, its content of glycogen could not amount to much. In very fat animals the insoluble remains of cuticle could not be filtered off until the samples had been acidified to remove impurities.

(d) *Calculation of results*

The suffix (1) refers to the control group and (2) to the flying group.  $L$  = total lipids in a group,  $R$  = total remainder (other dry matter),  $Q$  = total quantity combusted,  $d$  = deviation from mean percentage,  $n$  = number of individuals,  $v$  = sum of volume indices,  $w$  = initial group weight, and  $\Delta$  = error of the estimate of the initial amounts of fat and remainder in the flying group (in weight units).

Before flight the two groups were similar and  $v_1/v_2 = w_1/w_2$  (see §2(b)). The initial amounts of fat and remainder in the flying group could therefore be estimated from the amounts found by analysis of the control group, and since the analytical error was negligible

$$\Delta = w_2/100[\sum d_i^2/n(n-1)]^{\frac{1}{2}},$$

the initial

$$L_2 = w_2/w_1 L_1 \pm \Delta_L,$$

and the initial

$$R_2 = w_2/w_1 R_1 \pm \Delta_R.$$

According to this the amounts combusted equalled

$$Q_L = w_2/w_1 L_1 - L_2 \pm \Delta_L,$$

$$Q_R = w_2/w_1 R_1 - R_2 \pm \Delta_R.$$

From  $Q_L$  and  $Q_R$  the total energy expenditure, the share of fats and the metabolic rate could be calculated.

As an example experiment 2 is given in some detail. Each group numbered fifteen immature females; the flight lasted 4.50 h at an average speed of only 2.6 m/s, the deviations from the mean being small as seen in figure 4; the degree of truancy amounted to 10%:

$$v_1/v_2 = 96.3, \quad w_1/w_2 = 32.3/32.8 = 98.5, \quad \Delta_L = \pm 130 \text{ mg} \quad \text{and} \quad \Delta_R = \pm 100 \text{ mg},$$

the standard error of the mean percentage being  $\pm 0.4$  and  $\pm 0.3\%$  respectively (by fresh weight). The combustion amounted to:

$$\text{initial } L_2 = 2450 \pm 130 \text{ mg}$$

$$\text{final } L_2 = 1530 \text{ mg}$$

$$Q_L = 920 \pm 130 \text{ mg}$$

$$\text{initial } R_2 = 9360 \pm 100 \text{ mg}$$

$$\text{final } R_2 = 9130 \text{ mg}$$

$$Q_R = 230 \pm 100 \text{ mg}$$

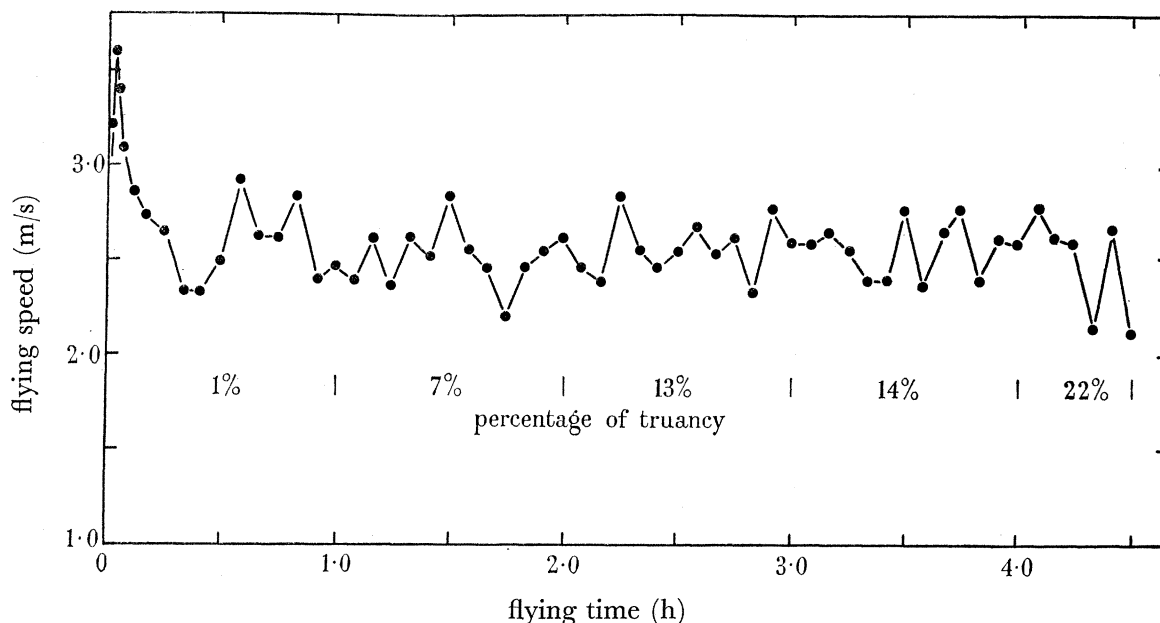


FIGURE 4. Variation in flying speed in the course of 4.5 h of uninterrupted flight of fifteen female *Schistocerca gregaria* (experiment 2). Each point denotes a reading. The percentages of trancy are given below the curve.

In the estimation of  $Q_R$  the faeces expelled by both groups were taken into consideration, the flying groups having dropped 323 mg (dry weight) against 18 mg in the control group. In the above calculation  $Q_R$  would therefore be about 305 mg too high if the faeces were not reckoned.

$920 \pm 130$  mg of fat and  $230 \pm 100$  mg of non-fatty substances were combusted and the metabolism could now be calculated because the remainder must be either protein or carbohydrate. As far as energy relationships are concerned, the following calculations are not influenced by the exact nature of the remainder fuels, the calorific value of protein and glycogen being nearly identical when oxidized in the organism. The conversion figures were taken from Carpenter (1939):

Energy derived from fats

$$9.5(0.92 \pm 0.13) \text{ kcal} = 8.74 \pm 1.24 \text{ kcal}$$

and from remainder

$$\frac{4.2(0.23 \pm 0.10) \text{ kcal} = 0.97 \pm 0.42 \text{ kcal}}{\text{total conversion } 9.7 \pm 1.3 \text{ kcal}}$$

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The probable maximum proportion of energy which was derived from fats thus amounted to

$$\frac{8.7 + 1.2}{8.7 + 1.2 + 1.0 - 0.4} 100 \% = 94 \%,$$

the minimum being

$$\frac{8.7 - 1.2}{8.7 - 1.2 + 1.0 + 0.4} 100 \% = 84 \%.$$

The average percentage from fat was 90 %. The oxygen uptake was calculated similarly giving  $2.04 \pm 0.27$  l. O<sub>2</sub>. The non-protein R.Q. was estimated from Carpenter's Table 13.

The metabolic rate of the 32.8 g of locusts amounted to  $73 \pm 10$  kcal/kg/h or to  $15.3 \pm 2.0$  l. O<sub>2</sub>/kg/h, the 10 % of truancy being taken into consideration.

## 3. RESULTS

(a) *Gross composition*

The chemical composition of locusts changes with age and external conditions and a single set of average figures would give a false impression of uniformity. Nevertheless, an attempt will be made to estimate the gross composition of full-grown, but immature desert locusts and to compare the amounts of stored fuel with the consumption during flight. The content of dry matter and ethereal extract of nine control groups is seen in table 6. Within a batch the standard errors did not exceed  $\pm 0.8$  % of the fresh weight, and so the batches differed significantly in composition. The average percentage composition of immature and mature locusts was calculated to the nearest whole number. It appears that the content of fat was somewhat lower in mature than in immature individuals; this has also been found in *Melanoplus* (Pfeiffer 1945). Only a few determinations of the fat content of desert locusts from nature are available, but Brodskis & Rungs (1944) found from 13 to 20 % by dry weight in different populations of various ages, i.e. from 5 to 8 % of the fresh weight. In pink immature *Schistocerca gregaria* of phase *gregaria* Brodskis (1944) found 8 % lipids by fresh weight, one-tenth of which was sterols. Thus the average lipid content of young migrants seems to be less than 10 %, and the average figures given in table 6 are reasonable for estimating the composition of young and well fed animals.

TABLE 6. PERCENTAGES OF DRY MATTER AND OF FAT OF NINE CONTROL GROUPS OF VARIOUS AGES

	batch no.	adult age (days)	no. of individuals	dry matter (% of fresh weight)	fat	
					(% of fresh weight)	(% of dry weight)
immature males	13	16	12	39.3	8.2	20.9
	7b	17	12	43.0	13.7	31.9
immature females	13	13	15	35.7	7.5	21.0
	7b	17	12	41.0	12.2	29.8
average content in immature locusts, <i>ca.</i>				40	10	25
mature males	5	33	7	37.0	3.9	10.5
	9	35	6	37.9	7.3	19.3
	12	43	6	36.5	6.5	17.8
	10	63	6	40.2	3.6	9.0
mature females	10	63	7	38.5	4.7	12.2
average content in mature locusts, <i>ca.</i>				38	5	13

From the point of view of storing reserve substances for flight, some parts of the animal can be considered of minor importance, i.e. legs, wings, cuticle, wing muscles and gut. The share of the appendages is summarized in table 7. It appeared that not less than a quarter of the total dry matter was contained in the legs and the wings, but by far the largest amount of fat (more than 90%) was found in the body. During the first 2 or 3

TABLE 7. DISTRIBUTION OF DRY MATTER, INCLUDING LIPIDS, IN THE PARTS OF THE LOCUSTS; AND PERCENTAGES OF LIPIDS IN THE DRY MATTER OF THE PARTS

	batch no.	dry matter, as % of total dry weight, found in			lipids as % of dry matter of the parts			
		body	legs	wings	total animal	body	legs	wings
males	13	71.1	20.8	8.1	20.9	27.3	4.6	7.9
	7b	75.2	17.9	6.8	31.9	39.0	7.1	8.9
females	13	74.5	16.8	8.7	21.0	25.9	4.4	7.1
	7b	77.4	15.1	7.7	29.8	34.6	8.6	8.9
average ca.		74	18	7	26	32	6	8

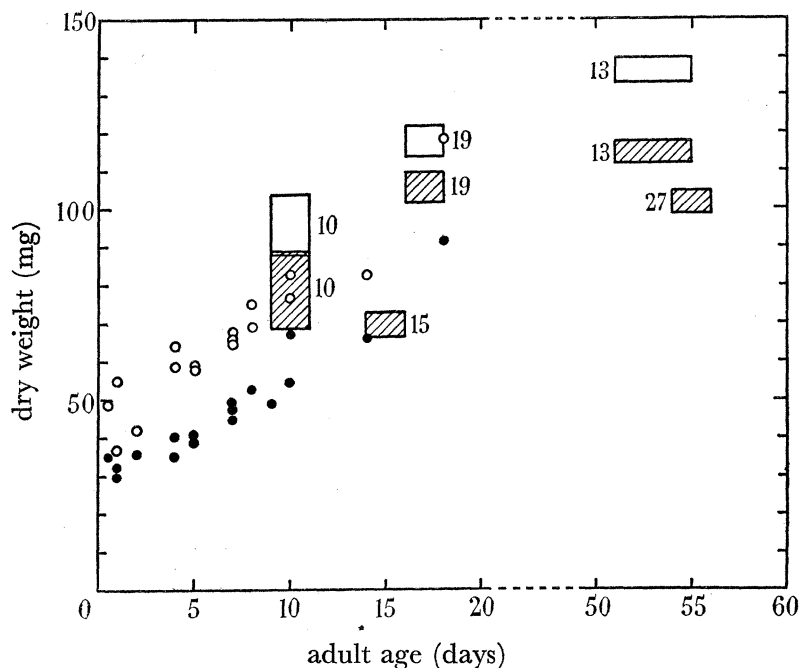


FIGURE 5. The prolonged chemical maturation of cage-bred *Schistocerca gregaria* as indicated by the increase in dry matter of body cuticle (white symbols) and of wing muscles (black and hatched symbols). All analytical results are recalculated for a standard *Schistocerca*. Figures near the rectangles show the numbers of animals, the sides denoting standard errors. The time scale is contracted between 20 and 50 days.

weeks of adult life, Pfeiffer (1945) found that the total amount of dry matter and fat of *Melanoplus* increased two or three times. Since the body cuticle and the wing muscles contribute considerably to the dry weight, and since they are both of direct importance for wing movement, the increase of these fractions was followed by analyzing individuals (101 in all) of various ages from five different batches. Figure 5 shows the increase in dry weight, calculated for a standard *Schistocerca*. Under laboratory conditions the pre-maturation accumulation of dry matter lasted 2 to 3 weeks, and the initial dry weight

was only about one-third of the final value. The fresh weight of the body (see figure 2) changed little, however, and therefore the power/weight ratio did not reach its full value until 2 or 3 weeks after the last moult. It is therefore not surprising that fledgling adults prefer to march with the hoppers and do not fly much. After 18 to 20 days of adult life the locusts can be considered fully developed, and it appears that a standard *Schistocerca* of that age contained 130 mg of body cuticle and 100 mg of wing muscles (dry weight). The importance of restricting the experimental work to full-grown but immature locusts is further emphasized by comparing mature males and females. The ratio of the weights of dry matter in the wing muscles of mature females and mature males was  $1.37 \pm 0.14$ , i.e. it corresponded to the ratio of the volume indices as well as of the fresh weights of immature locusts (see §2(b)). In contrast to this, the ratio of the weights of the two sexes in mature locusts was  $1.65 \pm 0.03$  (table 4), so that the increase in body weight of a mature female was not accompanied by a corresponding increase in muscle mass. The fat content and the muscle/weight ratio both indicated that migratory ability is greatest in fully developed but sexually immature locusts; in the laboratory such locusts fell into colour-group 3.

The average dry weight of the gut was 60 mg when the food remains were included. Concerning the ethereal extract, 160 analyses revealed that lipids never constituted less than 2% of the fresh weight of the whole animal (5% of the dry weight). The animals which contained only 2% would not fly (truants), but sometimes individuals which only contained 2.5% did fly. It was therefore concluded that less than 2% of lipids is incompatible with normal activity, this value being intermediate between the minimum values found in homoiothermal and poikilothermal vertebrates (Terroine 1920). About 2% of the ethereal extract was therefore regarded as indispensable lipid. Even after flight the locusts seldom contained less than 4%.

In table 8 is shown the average composition of the dry matter of a standard *Schistocerca*, estimated according to the above findings. The glycogen stored in the wing muscles cannot amount to much (see p. 22), and, since the fat content of the legs and wings was small, only two fractions remained which could contain significant amounts of fuel,

TABLE 8. AVERAGE COMPOSITION OF A STANDARD *SCHISTOCERCA GREGARIA*

The water content was 60 %.

	amount of dry matter	
	(% of total fresh weight)	(mg)
body: cuticle	6.3	130
wing muscles	4.8	100
alimentary canal*	2.9	60
remainder non-lipid	6.0	125
indispensable lipids	1.2	25
depot fat	8.4	175
total in body	29.6	615
legs: non-lipid	6.7	140
lipids	0.4	8
wings: non-lipid	2.9	60
lipids	0.3	6
total in legs and wings	10.3	214

\* Including dried contents.



namely, the 'remainder non-lipid' of the body and the 'depot fat'. However, the 125 mg of remainder contained the dry matter of the extrinsic leg muscles, the mandibular and the segmental muscles, the glands, the gonads, the hypoderm, the non-lipid parts of the fat body, etc. This means that only a part of it could be glycogen and, since the maximum value recorded so far has been 37 mg of glycogen (experiment 8), the stores of carbohydrates could hardly average more than 50 mg. By contrast, the average weight of fat was 175 mg. In other words, depot fat is clearly very important, for it contains at least 85 % of the total amount of stored energy.

(b) *Flight metabolism*

The main material consists of six experiments which are numbered in order of increasing flying speed. No attempt was made to use uniform batches, and table 9 shows how widely the batches differed in age, development and state of training. Moreover, both males and females were used, and in experiment 6 the animals were fed on kale instead of grass. If the results obtained with such heterogeneous 'swarms' have significant features in common they may be of general validity for flying locusts.

TABLE 9. BATCHES USED FOR FAT ANALYSES

experiment no.	batch no.	individuals per group; sex	adult age (days)	colour-group	no. of previous flights	food
1	12	6♂♂	40	6 to 7	3	grass + hay
2	13	15♀♀	13	3	1	grass + hay
3	13	12♂♂	16	3	1	grass + hay
4	7b	12♂♂	17	3	0	grass + hay
5	7b	12♀♀	17	3	0	grass + hay
6	5	7♂♂	33	6 to 7	13	kale + hay

*Flight performances.* In the above experiments, as well as in nos. 7 and 8, the climatic conditions were chosen as near to the optimum as possible. Nevertheless, flight differed considerably in both speed and duration, as is seen from table 10 and figures 6 and 7. On the other hand, during an experiment one gets an impression of uniformity in the intensity of flight. In order to make the average speed for the whole period valid as an estimate of the intensity of flight, the experiment was stopped if the speed dropped markedly. By this time, the locusts were generally by no means exhausted, as is indicated by the low percentages of truancy. The shapes of the curves were such that the arithmetic and the geometric means of the flying speeds were equal within  $\pm 0.1$  m/s; although the metabolic rate was found to increase approximately with the second power of the speed

TABLE 10. FLIGHT PERFORMANCES OF FLYING GROUPS

experiment no.	average speed (m/s)	flying time (h)	distance covered (km)	truancy (%)	temp. (°C)	water vapour deficit (mm Hg)
1	2.3	5.00	42	2	25.5	10.5
2	2.6	4.50	42	10	30.0	10.4
3	2.9	9.00	95	7	27.0	9.4
4	3.3	4.00	47	1	30.6	4.6
5	3.4	3.70	47	7	30.9	4.7
6	3.5	3.00	38	16	29	10
average	3.0	4.9	52	7	—	—

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(see p. 21), the average speed found in an experiment could be directly correlated to the metabolic rate, without any correction. The general sequence was similar in a large

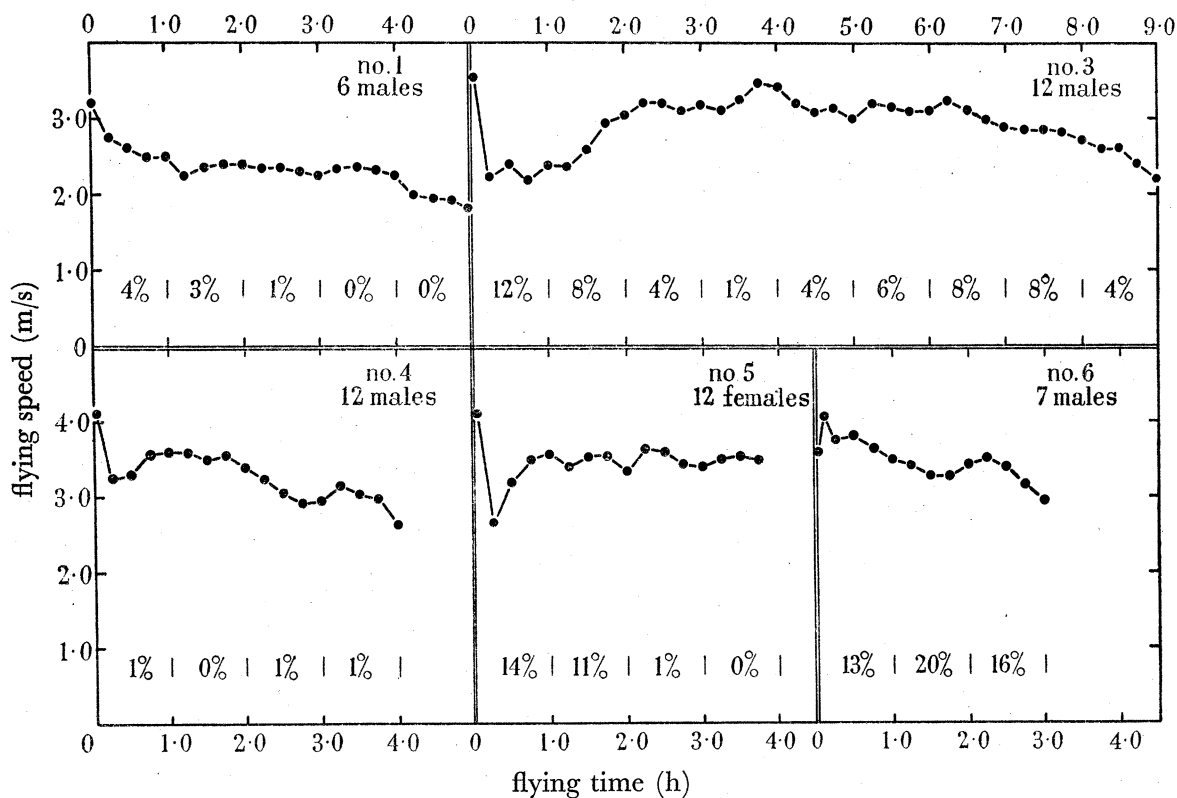


FIGURE 6. Flight performances of batches used for fat analyses; experiment 2 is shown in figure 4. Nos. 3 to 5 (above) and nos. 7 and 8 (figure 7) show the typical course. Each point denotes the average of three readings. The percentages of trauancy are given below each curve.

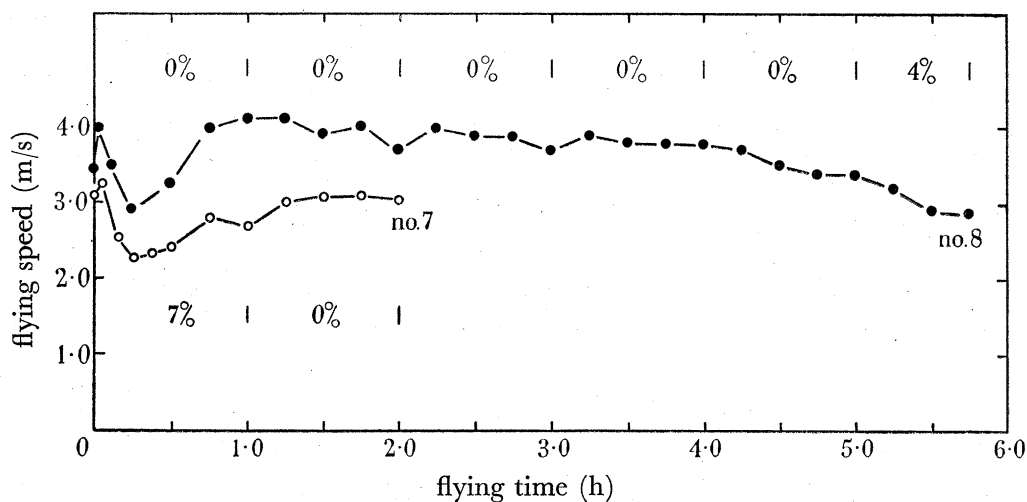


FIGURE 7. Flight performances of batches used for glycogen analyses. For explanation, see figure 6.

number of roundabout experiments, and two points are of special interest. First, the initial speed was high, in some cases exceeding 4 m/s, and it decreased rapidly during the following few minutes. Generally it reached a minimum about 15 to 30 min after take-off.

This decrease in speed was independent of trancy (see also figure 7) and occurred in single animals as well as in 'swarms'. It could therefore be regarded as typical of flight in the laboratory. Secondly, 30 to 60 min after take-off, the flying speed normally increased again until a cruising level was reached. Experiments 7 and 8 (figure 7) are typical in this respect and nos. 1 and 6 (figure 6) are exceptional.

The effect of temperature on the flying speed is shown in table 11, the mean, maximum and minimum average speeds being summarized from twenty-four roundabout experiments which all lasted for at least 2.5 h and which were performed at about 25, 30 and 35° C respectively. It is obvious that temperature had but little influence. Since no other climatic factor has yet been found which influences the speed significantly, it was fortunate that the eight experiments on fuels covered the total range of average speeds recorded from more than eighty experiments with the roundabout. The mean speed in experiments 1 to 6 was 3.0 m/s, i.e. near to the value of 2.8 m/s found in the experiments in table 11. The material was therefore representative as far as the flight performance was concerned.

TABLE 11. AVERAGE FLYING SPEEDS AT VARIOUS TEMPERATURES

temp. (°C)	no. of experiments	average duration (h)	average flying speeds (m/s)		
			average of all experiments	maximum av. recorded	minimum av. recorded
25 ± 1	5	3	2.8	3.0	2.5
30 ± 1.5	13	3	2.8	3.5	2.4
35 ± 1	6	3	2.8	3.0	2.6

TABLE 12. COMBUSTION OF FAT AND OF OTHER FUELS DURING FLIGHT

experiment no.	amounts of fuel metabolized (mg)			
	in group		per locust	
	fat	other fuels	fat	other fuels
1	240 ± 80	170 ± 50	40 ± 13	28 ± 8
2	920 ± 130	230 ± 100	61 ± 9	15 ± 7
3	915 ± 100	210 ± 50	76 ± 8	18 ± 4
4	980 ± 110	50 ± 100	82 ± 9	4 ± 8
5	790 ± 150	560 ± 140	66 ± 13	47 ± 12
6	260 ± 50	330 ± 60	37 ± 7	47 ± 9
		average <i>ca.</i>	60 ± 10	25 ± 8

*Fuels used.* Table 12 gives the amounts of fat and of other dry matter which disappeared during flight. In all cases the amount of fat decreased significantly, and in five (nos. 1 to 5) out of six experiments the main loss in dry weight was caused by combustion of fat. Except for experiment 4, however, a statistically significant amount of other dry matter also disappeared and must have been oxidized. Averages of about 60 mg of fat and 25 mg of other dry material was metabolized per locust. The contribution of the fat to the energy transformed was computed and the values are shown in table 13. In all cases at least two-thirds of the energy liberated was derived from fat. An average of not less than 80 to 85% must have been derived from stored lipids.

In mammals it has repeatedly been demonstrated that the excretion of nitrogenous waste products is practically unaffected by muscular exercise. The excess metabolism therefore

takes place at the expense of carbohydrates and fats. In locusts, fat is the predominant fuel for flight. Theoretically, however, the remaining fuel might be protein and not carbohydrate, especially when it is remembered that the concentration of free amino-acids is much higher in insect than in mammalian blood (up to 200 to 400 mg% non-protein nitrogen, see Wigglesworth 1950). Krogh & Weis-Fogh (1951) found that the R.Q. was 0.82 during the first 30 min of tethered flight and decreased to 0.75 during the succeeding hour. The main nitrogenous waste product of locusts is uric acid (Brown 1937). Combustion of protein alone would therefore give an R.Q. of about 0.80. If protein were the second most important fuel, practically all the energy should be derived from protein (or amino-acids) during the first half hour; later on, two-thirds (by weight) of the fuel should consist of protein. The first consequence can hardly be true, and the second statement contrasts with the results given in table 12; only about 30% of the fuel was non-lipid. Moreover, table 13 shows that in the six experiments the calculated values of the R.Q. agree with the results obtained by gas analyses, it being assumed that all the remaining non-lipid fuel consisted of carbohydrate. The average R.Q. from the roundabout

TABLE 13. FAT AS A SOURCE OF ENERGY FOR WING MOVEMENTS; AND THE R.Q. CALCULATED ON THE ASSUMPTION THAT THE REMAINING FUEL IS CARBOHYDRATE

experiment no.	percentage of energy from fats			calculated non-protein R.Q.		
	mean	min.	max.	mean	min.	max.
1	77	62	86	0.77	0.75	0.82
2	90	84	94	0.74	0.72	0.75
3	91	87	93	0.73	0.72	0.74
4	98	93	100	0.71	0.70	0.73
5	78	70	84	0.77	0.75	0.79
6	64	54	73	0.81	0.78	0.84
average	83			0.76		

experiments thus averaged 0.76 against 0.75 found by gas analyses. The probable range of the R.Q. was also identical in the two cases, and it was concluded that fat and carbohydrate were the predominant fuels.

The question arose whether blood glucose was of any significance as a fuel reserve, for Beutler (1937) has demonstrated that fasting bees must rely entirely upon the sugar dissolved in the circulating blood. In various bees she found exceptionally high blood-sugar concentrations (2% or more). But in grasshoppers of the genera *Melanoplus* and *Chortophaga*, Blumenthal (1927) found only 0.05%. Preliminary determinations of the reducing power of blood of four resting *Schistocerca gregaria* males (determined on 0.05 ml. blood by the Hagedorn-Jensen method (Hagedorn *et al.* 1946)) gave values equivalent to 0.22 to 0.24% glucose, part of which may not be sugar (Hemmingsen 1924). Since the blood volume hardly exceeded 0.2 ml. per animal, not more than 0.5 mg glucose could be present in the blood, i.e. the blood sugar could provide the energy for 1 min of flight at the most. On the other hand, the glycogen content of the same four animals ranged from 16 to 33 mg. The carbohydrate reserve thus consisted of glycogen. It was therefore of interest to see how much of the non-lipid material used up during flight could be glycogen. Accordingly, two roundabout experiments (nos. 7 and 8) were carried out in the usual way, but glycogen was investigated instead of fat. Sixteen newly matured males were used in

both cases (colour-groups 4 to 5 in no. 7, and colour-group 6 in no. 8). The flight performances are seen in figure 7. In experiment 7 eight locusts flew at moderate speed and were stopped after 2 h. In experiment 8, however, flying was extraordinarily intense (3.7 m/s) and the animals were far from being exhausted when they were stopped after nearly 6 h. The amounts of glycogen found in the control groups and in the flying groups are shown in table 14. In both experiments all the animals that had flown contained very little reducing material after alkali treatment, corresponding to only 2 mg glycogen. In the controls the amounts ranged from 3 to 6 mg in experiment 7 and from 6 to 37 mg in experiment 8. In the latter case  $121 \pm 36$  mg glycogen was combusted by the flying group, i.e. about  $17 \pm 5$  mg per standard *Schistocerca*. Thus a consumption of glycogen was

TABLE 14. GLYCOGEN CONSUMPTION DURING FLIGHT

experiment no.	content of glycogen (mg)				glycogen consumed per locust (mg)
	controls		after flight		
	in group	per locust	in group	per locust	
7	36	$4.5 \pm 0.4$	17.8	$2.2 \pm 0.2$	$2.3 \pm 0.5$
8	137	$17 \pm 4$	15.6	$1.9 \pm 0.1$	$15 \pm 4$

directly demonstrated which was of the same order of magnitude as indicated in table 12 ( $25 \text{ mg} \pm 8$ ), the conclusion being that the 'remainder fuel' consisted of glycogen. The low reducing power found after flight as well as the surprisingly low variation ( $\pm 0.1$  to  $\pm 0.2$  mg glycogen) show that the available stores of glycogen were exhausted during flight. Furthermore, when small pieces of the fat body were stained with iodine (experiment 8) no sign of glycogen appeared in locusts that had flown, though it could readily be demonstrated in the controls. According to the calculation on p. 23 a standard *Schistocerca* uses an average of 8 to 9 mg of glycogen during the first half-hour of flight, so that the reserves probably disappear within 1, or at most 2 h. In spite of that, the flying speed was generally maintained. When calculating the total conversion of energy in experiment 8 (see p. 22), it was found that the glycogen consumed could only account for one-twentieth of the energy utilized. During most of the 6 h fat alone must therefore have supplied the necessary energy.

*Metabolic rate.* Table 15 gives the average metabolic rates calculated both as large calories (kcal) liberated and as litres of oxygen consumed per kg body weight per hour. The rates varied between 50 and 140 kcal/kg/h or between 10 and 30 l. O<sub>2</sub>/kg/h. In other words, during tethered flight in a respiration chamber (Krogh & Weis-Fogh 1951) the oxidative processes were as intense as in these more freely flying animals. These rates can be correlated with the flying speed. This is illustrated in figure 8, the error of the single determinations being indicated. Experiment 2 deviated somewhat from the other results, but the females in question were the youngest used (13 days after emergence, table 9) and their average weight was 16% less than should be expected from their volume index. The other groups were of standard weight within  $\pm 5\%$ . In roundabout experiments the lift could not be taken into account, and the power necessary to revolve a group at a certain speed depended upon the size rather than on the weight of the animals. It was therefore reasonable to recalculate the value found in experiment 2 to animals of standard weight, the result being indicated as a cross in figure 8. The curve drawn indicates that

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TABLE 15. METABOLIC RATES AT VARIOUS FLYING SPEEDS

experiment no.	average flying speed (m/s)	metabolic rate per unit body weight	
		power expenditure (kcal/kg/h)	oxygen consumption (l. O <sub>2</sub> /kg/h)
1	2.3	47 ± 14	9.5 ± 2.7
2	2.6	73 ± 10	15.3 ± 2.0
3	2.9	57 ± 6	12.0 ± 1.2
4	3.3	107 ± 12	22.8 ± 2.7
5	3.4	110 ± 15	21.2 ± 3.4
6	3.5	140 ± 22	28.5 ± 4.0

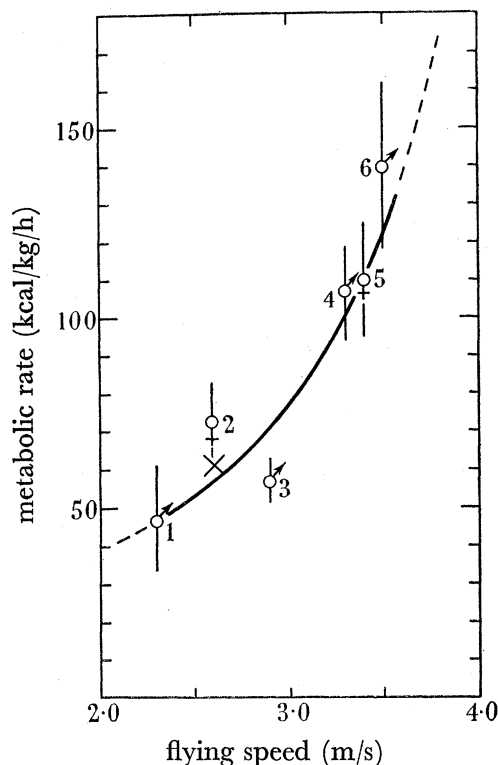


FIGURE 8. The relation between the flying speed in the roundabout and the metabolic rate calculated as large calories converted per kg fresh weight per hour. The estimated errors are indicated. For further explanation, see text. The metabolic rate increased approximately as the square of the speed.

the power output increased approximately as the second power of the speed. However, the accuracy did not allow any detailed treatment. A third-power relationship might have been expected because the air resistance of an element is proportional to the second power of the speed. The sum of the integrated energy losses due to wing inertia, air resistance, thoracic damping, etc., might also approximate to a second- or third-power relationship, but no attempt will be made to interpret the curve in mathematical terms because the necessary fundamental knowledge is lacking on which the single integrations and their possible mutual interrelations should be based.

The curve shows that, on the roundabout, increased speed means greater cost per km. By means of figure 8 it is possible to predict the metabolic rate of a 'swarm' from its flying speed and thus to compare different flight performances in terms of power output. During the first few minutes of flight, the speed often exceeded 4 m/s; by extrapolating

the curve it is seen that the metabolic rate often then rose above 200 kcal/kg/h, i.e. the oxygen consumption corresponded to 40 to 45 l. O<sub>2</sub>/kg/h. It is reasonable to suggest the extraordinarily high metabolic rates of 200 l. O<sub>2</sub>/kg/h recorded in flying Lepidoptera by Raffy & Portier (1931) to be maximum values, for their experiments lasted only 1 min. In general, results obtained during the first few minutes of flight should be interpreted with caution, because the power output might be several times higher at that time than during sustained flight. The average speeds recorded in ordinary roundabout experiments were equally distributed around the mean value of *ca.* 3 m/s, the speed to which the following calculations refer. At this speed the power output corresponded to 75 kcal/kg/h and the oxygen intake to 16 l. O<sub>2</sub>/kg/h. During the first 5 h 85 % of the energy came from fat, and the fuel used would amount to 6.7 g fat + 2.7 g. glycogen/kg/h. In other words, a standard *Schistocerca* (2.1 g) on an average used up 14 mg fat + 6 mg glycogen/h = 20 mg dry fuel/h. This hourly consumption corresponds to 1 % of its fresh weight or 2.5 % of its dry weight. During the first 5 h, and probably early in that period, the stores of glycogen would have been used up and fat would be the only remaining fuel; 17 mg of fat would then be oxidized per hour, or 0.8 % of the fresh weight.

(c) *Mobilization of fuels*

According to table 12, 70 to 110 mg dry matter had disappeared per locust during flight. The average sizes of the animals in question were very near to the standard size, and the above figures therefore indicate the consumption of fuel during an average performance. Since the wing muscles of a standard locust contain 100 mg dry matter (table 8) an ordinary flight requires as much material to be transported to the muscles as they themselves contain; and, in terms of energy, the muscles converted about twice as much energy as was contained in the constituent proteins and the stored glycogen together. Prolonged flight must therefore largely depend upon the movement to the wing muscles of fuel stored elsewhere in the body. No investigation has been made of the state in which fuels are transported, but some few outlines of the nature of mobilization will be treated.

Microscopic observations revealed that fat was stored to only a small extent in the wing muscles. Glycogen was not quantitatively isolated from these muscles. But knowing the metabolic rate, the maximum share of muscle glycogen could be estimated as follows. In striated muscles of vertebrates, glycogen seldom constitutes more than 1 % of the fresh weight, though Schoendorff (1903) found more than 3 % in dogs which were given excessive amounts of carbohydrate after a period of starvation. Before flight the thorax of the blowfly *Lucilia sericata* on an average contained 3.4 % glycogen (Williams, Barnes & Sawyer 1943), which must have been stored mainly in the wing muscles. According to the maximum values recorded so far, 3 or 4 % of muscle glycogen can be regarded as the largest capacity. Since the water percentage of the wing muscles of *Schistocerca gregaria* ranged from 71 % in old animals to 74 % in young adults, the maximum amount of glycogen in these muscles could be estimated not to exceed 12 to 14 mg. During 5 h of average flight a standard *Schistocerca* could get, from this source, at the most 6 to 8 % of the total energy necessary. According to figures 6 and 8 the average combustion during the first 30 min of flight amounted to 85 kcal/kg/h. In the same interval the R.Q. varied about 0.8 (Krogh & Weis-Fogh 1951), and 40 % of the energy was derived from carbo-

hydrates. A standard locust would therefore use 5.6 mg fat and 8.5 mg glycogen during the initial half-hour. In other words, the glycogen deposited in the wing muscles might be used up in less than 30 min after take-off. As mentioned before, the flying speed generally decreased after the first 10 min of intense flight, a minimum being reached in 15 to 30 min. After that time a second increase in speed took place. These observations fit the hypothesis that, to begin with, the muscle glycogen is especially drawn upon, and when this store becomes depleted a decrease in speed occurs until the mobilization of fuel, especially fat, from more remote parts of the body becomes adequate.

The legs and the wings of insects are not generally regarded as storage organs. But the fuel delivered from these parts may not be quite negligible. This is illustrated in table 16. Only experiments 2 and 3 were sufficiently detailed to be applicable. No statistical treatment could be undertaken because the legs and the wings were weighed and extracted *en bloc*. It is noteworthy, however, that in all cases a decrease was observed in the dry matter of the appendages of the flying groups. The total loss from the appendages amounted to 4 to 5% of the dry weight, but not less than 25 to 30% of the content of lipid had disappeared from both legs and wings. The mobilization of fuel was therefore of a general nature, so that even the remote cells present along the veins of the wings must have released stored fat and glycogen. It is interesting to note that Wigglesworth (1949) found a considerable concentration of glycogen in the modified hind wings of Diptera, the halteres. Moreover, this store was drawn upon during flight, and we can generally conclude that both glycogen and fat can be mobilized via the blood from all depots present. From table 16 it appears that the appendages provided about 3 mg fat and 5 mg remainder fuel used by an individual. But in a 5 h period this amount corresponded to only 6% of the total energy expended.

TABLE 16. MOBILIZATION OF FUEL FROM LEGS AND WINGS

experi- ment no.	no.; sex	dry matter mobilized per group (mg)				fuel mobilized from appendages per locust (mg)		percentage of total energy expenditure derived from appendages (%)
		from legs		from wings		fat	remainder	
		fat	remainder	fat	remainder			
2	15♀♀	18	30	20	20	2.5	3.3	6
3	12♂♂	16	55	16	19	2.7	6.2	6

The total amount of fuel mobilized from the wing muscles, the legs, and the wings could account for 10 to 14% of the energy at most. During sustained flight the locusts must therefore rely upon the energy stored in the fat body. The fat body of *Schistocerca* consists of a reticulated carpet composed of units 0.2 to 0.3 mm wide. It envelops the organs throughout the body, and its large surface and wide distribution make it well adapted for releasing stored materials.

In order to give an impression of the importance of the different depots, the results from experiment 3 are illustrated in figure 9. This shows the amounts of energy contained within the various parts of locusts in the control group (white) and in the flying group (shaded). Before the experiment the two groups did not differ more than 1% in fresh weight and volume index. It is assumed that no combustion of the wing muscles themselves took place, and their content of glycogen was regarded as contained in the



'remainder non-lipid'. The dominating importance of the fat content of the body is obvious, but a reduction of lipids in the appendages is also evident, especially when it is remembered that a great part of their original content must be indispensable lipids.

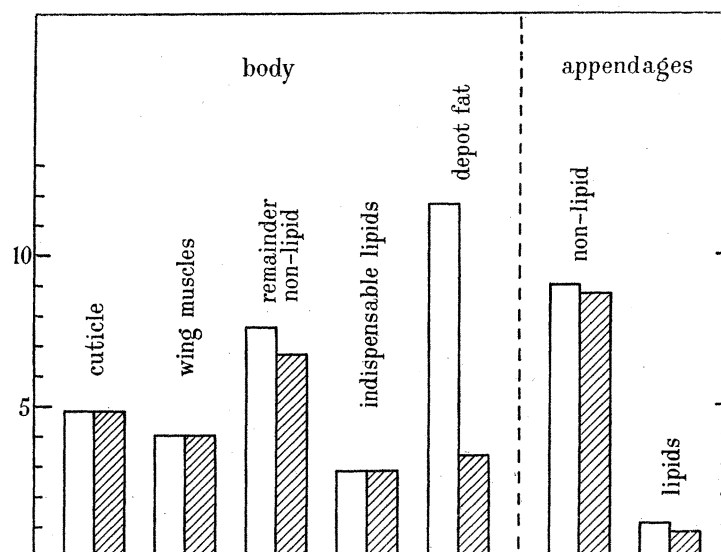


FIGURE 9. Experiment 3: estimated amounts of energy (kcal), as would be determined in a bomb calorimeter, in various parts of the control group (white columns) compared with the corresponding amounts in the flying group after 9 h of flight (shaded columns). Before flight the two groups were practically alike. By far the largest share of the expended energy came from depot fat in the body, but even the legs and wings contributed noticeable amounts.

#### 4. DISCUSSION

Water, heat and weight economy of flying locusts depend on the metabolic rate and on the nature of the fuels utilized, but these items will be discussed elsewhere (cf. Weis-Fogh 1952), and the present discussion will deal mainly with such problems of migration as are directly related to the amounts and nature of the combusted fuels. In addition, the performance of the wing muscles will be compared with that of other muscles, in order to discuss some general problems related to intensive utilization of fat.

##### (a) *Applicability of results*

When estimating the consumption of fuel of natural swarms it is essential that the experimental animals should not differ much from natural migrants. Since analyses of fat and glycogen of true migrating locusts before and after flight are lacking, application of the present conclusions might be misleading. The following remarks make it reasonable, however, that the main results are representative of migrations in nature. Thus the experimental animals resembled true migrants in having the coloration of phase *gregaria* and the biometrics of phase *transiens*. As to the optimum age for migration, Kennedy (1951) regarded both fledglings and sexually active desert locusts as 'semi-migrants'. Thus fledglings were unable to maintain vigorous flight, and mature adults did not take to the wing as readily as full-grown but sexually immature 'full migrants'. The same was observed in the laboratory (p. 6) and could be related partly to the relatively slow development of body cuticle and wing muscles of newly hatched adults, lasting for 2 or

even 3 weeks (p. 14), and partly to the considerably increased weight of mature females, the increase of weight being not compensated for by an increased muscle mass (p. 15).

Concerning the duration of flight, the flying times recorded in the roundabout (cf. table 10) compared well with the few observations from nature (Gunn *et al.* 1948). In the laboratory, the endurance turned out to be influenced by the humidity of the air, and the longest performances were obtained when the water-vapour pressure within the thoracic air sacs did not differ more than 15 to 20 mm Hg from the vapour pressure of the surrounding air, the air within the tracheal system being assumed saturated with water at 3° C above room temperature. A rise in the body temperature of this order of magnitude was found in some preliminary measurements made by the technique described by Krogh (1948).

On the roundabout, temperature did not influence the flying speed (cf. table 11), and it was therefore not possible to control the intensity of flight. In using roundabout experiments for studying the metabolic rate one could object that the flying speeds recorded at a certain power output did not correspond to the average air speed obtained under natural conditions, but as also discussed by Krogh & Weis-Fogh (1952), discrepancies may be considered small. By comparing his measurements in the field with those of other investigators Kennedy (1951) concluded (pp. 177 and 223) that the cruising air speed of *S. gregaria* varied between 2.5 and 4 m/s, i.e. within the same limits as found in the roundabout. Although, in a single series of measurements, Waloff & Rainey (1951) estimated the average air speed to be about 5 m/s, it is reasonable to suppose that the intensity of flight in the laboratory did not differ much from the intensity of free flight occurring in nature. In any case, the values obtained by means of the roundabout were mutually comparable since in all experiments the animals were suspended in the same way, i.e. from the pronotum, and the flying speed could be taken as an average measure of the intensity of flight. Since the speed depends upon the net effect of the moving wings it is a better indicator than would be any single parameter, as for instance wing-beat frequency.

Phase, optimum age, duration and flying speed therefore resembled what have been found in nature, and the results and conclusions arrived at may be applied to true migrants.

#### (b) *Swarm behaviour*

In the morning the activity of the basking locusts gradually increases and more and more individuals take to the wing, settling again after a while (Gunn *et al.* 1948; Kennedy 1951; Waloff & Rainey 1951). One or two hours before mass departure, milling and surging of smaller groups generally occur. This means that most locusts have flown for some time before proper migratory flight starts; after take-off, one would therefore not expect to find the initial decrease in flying speed which was so typical for the experiments in the laboratory. Since a large part of the glycogen is used up during the first half-hour of flight, this milling behaviour would tend to empty the stores of carbohydrates before proper migration starts. According to the hypothesis on p. 23 the preparatory flying would intensify the mobilization of fuels, especially of fat, from depots outside the wing muscles. In other words, surging and milling may bring forward the mobilization of fat so that the full metabolic requirements can be met by fat when proper migration starts.

In the laboratory the main part of the faeces were expelled during the first half-hour of flight, and it is interesting that hoppers of the migratory locust (*Locusta migratoria* L.) become the more excitable and more ready to march the smaller is the amount of material they carry in the gut (Ellis 1951). Concerning adult *Schistocerca*, 24 h of fasting caused a decrease of the respiratory quotient of resting animals from about 0.8 to 0.7 (unpublished), and such locusts were very active and excitable when basking in the cage. So it may be that both emptying of the gut and the change from a mixed supply of fuel to a fuel in which fat predominates intensify the general excitement on which mass departure depends.

(c) *Duration of flight*

In nature flight activity before mass departure probably depletes glycogen, so that the migratory flight takes place at the expense of fat. The amounts of energy converted in experiments 1 to 6 (table 12) were calculated, and the theoretical average durations of the performances were estimated from the average metabolic rate at 3 m/s. To these figures were added the possible additional flying times as estimated from the amounts of depot fat found after flight. The resulting maximum flying time at 3 m/s, i.e. the endurance, is seen in table 17, and figure 10 shows the relationship between the calculated endurance and the initial fat content. Varying contributions made by carbohydrate would cause the points to deviate from a straight line, but in the present experiments such deviations were but small; the endurance of a swarm could therefore be taken as proportional to the average percentage of fat before the take-off. Since the initial load of fat did not exceed 16% of the fresh weight, the reduction in weight during the exercise need not be considered in these rough estimates. It is seen that a standard *Schistocerca* (10% fat) should be able to

TABLE 17. CALCULATED MAXIMUM DURATION OF FLIGHT AT 3 M/S

experiment no.	energy expenditure demonstrated (kcal/kg)	corresponding flying time (h)	depot fat found after flight (g/kg)	further flying time possible (h)	total flying time possible (h)
1	235	3.1	38	4.8	8
2	328	4.5	36	4.6	9
3	512	6.8	25	3.2	10
4	428	5.7	84	10.6	16
5	407	5.4	89	11.3	17
6	420	5.6	5	0.6	6

fly for about 13 h, whereas a medium fat locust (8%) could not fly continuously for more than 10 h. Under suitable climatic conditions exceptionally fat locusts (15 to 16%) should be able to fly for about 20 h at medium intensity, but continuous flight of that duration must be at the upper limit. Discontinuous (rolling) flights lasting for 4 to 8 h were reported by Gunn *et al.* (1948), but trustworthy information on longer flights is scarce. Waloff (1946), however, concluded from various observations that a swarm of desert locusts had crossed the ocean between southern Morocco and Portugal (600 miles) with the aid of the wind, and that it must have been on the wing for about 24 h. It must be borne in mind in this case that a good deal of gliding flight (Rainey & Waloff 1951) may have occurred and that many of the locusts may have been drowned.

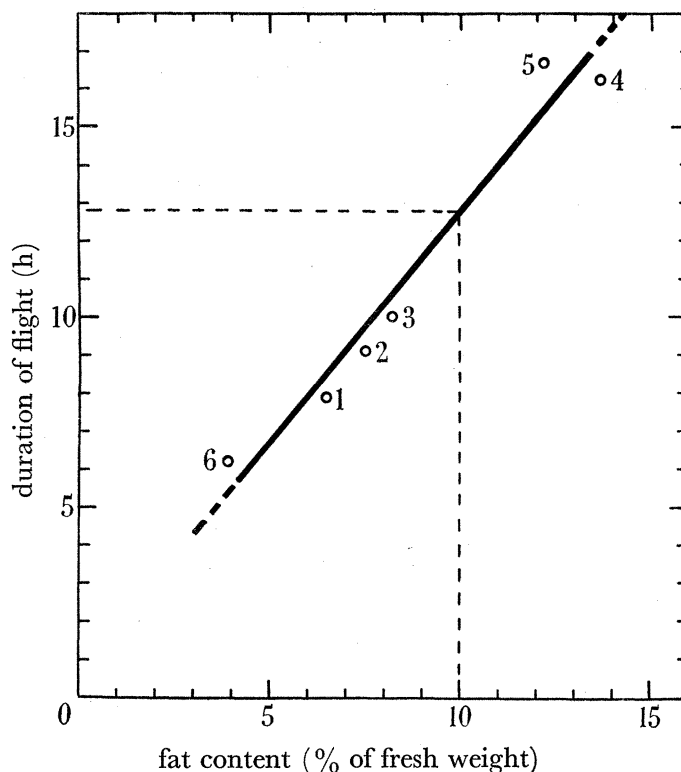


FIGURE 10. The calculated maximum duration of uninterrupted flight at 3 m/s plotted against the initial fat percentage (experiments 1 to 6). Even when a relatively large amount of carbohydrate is used (nos. 5 and 6) the endurance is nearly proportional to the initial fat content.

(d) *Food requirements*

Mass departure often starts 2 or 3 h after sunrise and flight may continue more or less continuously throughout the day (Gunn *et al.* 1948; Kennedy 1951). Migrations of 5 to 8 h duration are thus common (cf. Waloff & Rainey 1951). Per day this corresponds to an energy expenditure of 300 to 600 kcal/kg for flight only, while the metabolism during the period of rest would amount to one-tenth of this figure (Krogh & Weis-Fogh 1951). The content of digestible protein, fat and carbohydrate in ordinary vegetables (Groth-Petersen 1940) as well as in various grasses (Rasmussen 1941) corresponds to 300 to 500 kcal/kg fresh weight, the coefficient of digestibility being based upon experiments with ruminants. The utilization of food in phytophagous insects is usually small (Evans 1939, 30 % in some lepidopterous larvae), and the rapid digestive rate and the short and simple alimentary canal of Acrididae both suggest a low degree of utilization (cf. Uvarov 1948). If the average duration of flight is 5 to 8 h a swarm must therefore eat at least one to one and a half times its own weight every day and probably two or three times as much. In some areas, as in the Kenya Highlands, rolling migration frequently occurs (Gunn *et al.* 1948); some feeding can then take place during non-flying periods (information from Dr D. L. Gunn), so that output and input of energy may balance even during migration. During continuous flight or when a swarm passes over barren grounds or crosses the sea, however, the locusts would have to consume very considerable amounts of food in the periods of activity after settling in the evening and before flying starts in the morning;

low temperatures during the night may then delay feeding. Under certain conditions, the consumption rate seems to be a limiting factor as revealed from figure 11. It shows three experiments from three succeeding days (I to III) with the same ten females which had recently matured. After each flight they had access to abundant fresh kale for at least 4 to 6 h before the light was turned off and the food removed for the night. The first day (I) they flew normally for 4 h and with only 3% of truancy. The next day (II) they started as before, but 30 min after the start the speed had decreased to 2 m/s, the truancy exceeded 30%, and the experiment was stopped. The animals were then returned to the cage and fed. The ability to endure sustained flight was regained the following day (III). A similar effect of relatively short flights could not be demonstrated in males. It looked as if the depots of fuels of egg-producing females cannot always be restored between settling in the evening and daylight next morning on account of competition between the simultaneous storing in the fat body and in the ovaries. Lack of time for feeding and digestion rather than an adaptive mechanism might explain why Gunn *et al.* (1948) found that locusts started later in the morning when the previous day had been warmer than normal, i.e. when temperature had favoured flights of long duration in the Kenya Highlands. Besides the direct effect of air temperature, radiating heat, etc., on the ability to fly, it was therefore suggested that the condition of a swarm and the possibilities for feeding are significant factors in determining when the swarm will take off and how long it will go. This was also suggested by Waloff & Rainey (1951).

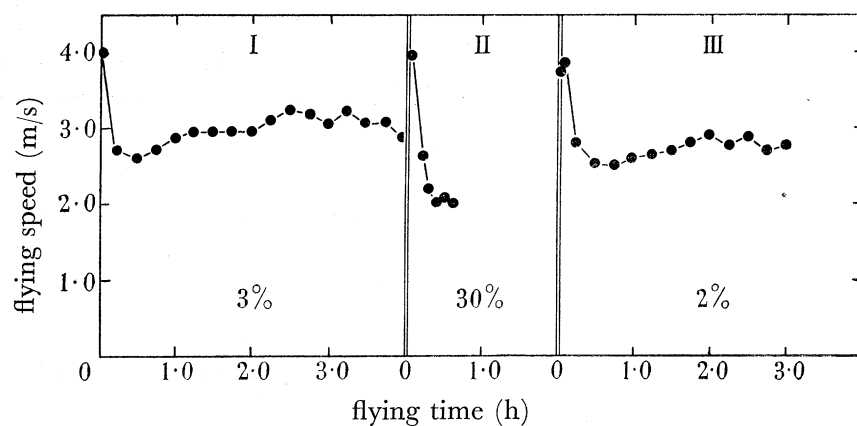


FIGURE 11. Three experiments performed with the same ten mature *Schistocerca gregaria* females on three succeeding days. They indicate that the food consumption might be too small in egg-producing females to allow for daily migrations, for on the second day the proportion refusing to fly (truants) quickly reached 30%. The experiment was therefore stopped and on that day more time was allowed for feeding. By the following day, recovery appeared to be complete.

A large swarm of desert locusts was estimated to weigh 13000 to 19000 tons (Gunn *et al.* 1948). The daily combustion of fuel of this swarm would correspond to 500 to 800 tons of fat, and per day it would demand as many calories as would 1.5 million human beings. Medium swarms are about one-tenth the size, but the figures are still considerable.

(e) *Optimum cruising speed*

The relationship between fuel consumption and air speed of aircraft is far from being simple and involves several parameters. This must also be the case in flying animals, but

## METABOLISM OF FLYING LOCUSTS

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our present knowledge is too restricted to allow for a detailed treatment of the results presented in figure 8. Since, however, no such results have been published before, it is worth while to compare aircraft and insects, and figure 12 shows the relationship between 'metabolic rate' and air speed in two modern airplanes equipped with variable-pitch propellers (information from the manufacturers' pamphlets). Within the recommended range of speeds, i.e. between 250 and 310 km/h, fuel consumption varied nearly linearly with speed, so that the cost of aerial transport (kcal/kg/km) remained approximately constant. But the fuel economy deteriorated considerably at speeds above 310 km/h.

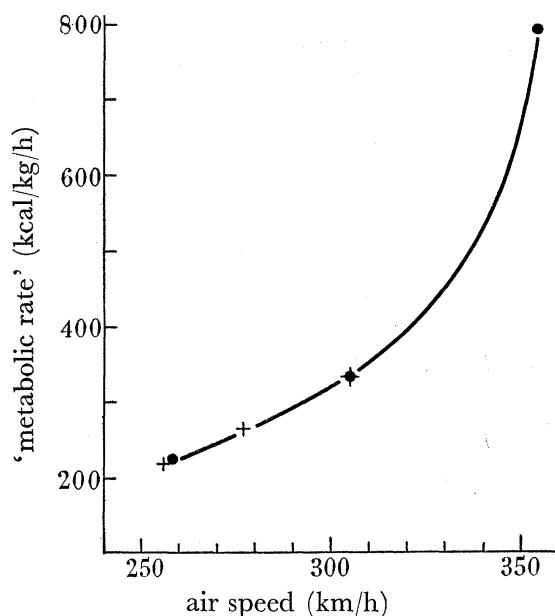


FIGURE 12. Relative power output (= 'metabolic rate') of two propeller-driven airplanes when flying at various speeds. The highest speeds could be maintained for only a few minutes.  
 ● Bristol Freighter Type 170 (16.8 tons). + De Havilland Dove (3.9 tons).

In other words, aircraft fly economically only within the rather narrow range of speeds for which they have been designed, and by comparing figure 12 and figure 8 the same seems to be the case in locusts, at least when they fly in the roundabout, performances at 2.5 m/s being two or three times less expensive than at 3.5 m/s. According to figure 8 the lowest speed at which locusts can develop sufficient lift to remain airborne would be the optimum speed for long-range migrations. In this connexion it is interesting to note that migrating dragonflies fly more slowly than the solitary hunting individuals (Federley 1908; Nordman 1935; Larsen 1950).

(f) *Metabolism of wing muscles*

The metabolic rate of the wing muscles can be calculated from the total power output of the insect when the ratio between muscle weight and body weight is known because the metabolism of the wing system is twenty to hundred times larger than the metabolism of the remaining tissues. Since preliminary estimates gave higher ratios than found by Magnan (1934) the weights of the wing muscles of some representative insects were estimated by multiplying their content of dry matter by  $\frac{10}{3}$ , the water content being always near to 70%. In *Schistocerca gregaria* the wing muscles were thus found to constitute 18%

of the body weight (see figure 5), in *Apis mellifica* 17 % (thirty honey-collecting workers), and in *Calliphora erythrocephala* 35 % (fifty adults, 1 week old). In *Drosophila repleta* the figure is 18 % according to Chadwick & Gilmour (1940), and 25 % being intermediate between the values found in the above flies, this figure was thought to be representative for *Lucilia sericata*. According to a single analysis the pectoral muscles of humming birds (unknown species) constitute about 40 % of the body weight. These ratios were used for calculating table 18, which shows the metabolic rate of some muscles on which sufficient

TABLE 18. APPROXIMATE METABOLIC RATES OF VARIOUS MUSCLES WORKING AT MAXIMUM (max.) OR AVERAGE CONTINUOUS (av.) POWER OUTPUT

animal	type of muscle	metabolic rate (kcal/kg/h)	predominant fuel	references
man	leg	max. 50 to 60	carbohydrate + fat	Asmussen <i>et al.</i> (1939)*, Krogh & Lindhard (1920)
	heart	max. 60 to 100	carbohydrate	Brody (1945)*, Katz (1932)*, Cruickshank & Startup (1933)
hummingbirds ( <i>Calypte</i> sp., <i>Selasphorus</i> sp.)	wing	700 to 1000 (short flights)	?	Pearson (1950)*
locust ( <i>Schistocerca gregaria</i> )	wing	av. 400 to 800	fat	Weis-Fogh (1952)*
fruit fly ( <i>Drosophila repleta</i> )	wing	av. 650	carbohydrate	Chadwick & Gilmour (1940)*, Williams <i>et al.</i> (1943)
blow fly ( <i>Lucilia sericata</i> )	wing	av. 1700	carbohydrate (fat?)	Davis & Fraenkel (1940)*, Williams <i>et al.</i> (1943)
bee ( <i>Apis mellifica</i> )	wing	av. 2400	carbohydrate	Jongbloed & Wiersma (1935)*, Beutler (1937)

\* Estimates of the metabolic rate.

information was available. The very high continuous power output of wing muscles is striking compared with the maximum rates of human muscles. In locusts, for example, wing muscles normally convert energy ten to fifteen times more intensely than the leg muscles of a well-trained man (Asmussen, Christensen & Nielsen 1939). It is also suggestive that the indirect wing muscles of some Diptera and Hymenoptera convert energy at an average rate of 2000 kcal/kg muscle/h, the corresponding values for modern aircraft engines of the piston type being 2000 to 4000 kcal/kg/h at maximum continuous power output. Thus the potential properties of striated muscles would not prevent flying of large animals, but, apart from other serious objections as to design and dimensions of large flying animals, the problem of heat economy would have been difficult if not impossible to solve.

Table 18 shows that wing muscles of locusts can utilize fat at much higher rates than formerly demonstrated in striated muscles. Wigglesworth (1949) assumed that fat could not be oxidized at a sufficient speed to provide energy for *Drosophila* when flying, but it is seen that its muscles do not work at higher rates than those of *Schistocerca*. It therefore seems to be qualitative rather than quantitative factors which make fat inapplicable in flying *Drosophila* and of outstanding importance in *Schistocerca*. According to our present knowledge the wing muscles of other Diptera as well as of Hymenoptera generally demand carbohydrate and cannot make use of fat when working. These muscles are highly specialized (see Wigglesworth 1950), and recently Watanabe & Williams (1951) advanced

much evidence in favour of regarding the so-called sarcosomes as giant mitochondria. The sarcosomes are densely packed along the fibrils, and they were shown to contain many enzymes that are characteristic of oxidations taking place via the citric acid cycle. In this and many other respects they resembled mitochondria from vertebrate tissues, although they are considerably larger (cf. Harman 1950). Mitochondria from liver cells of mammals can oxidize fatty acids at considerable intensity (Kennedy & Lehninger 1948; Schneider 1948). It might therefore be that the mitochondria of the specialized wing muscles of flies, wasps and bees have lost the ability to initiate breakdown of fatty acids, in contrast to the remaining tissues (Wigglesworth 1949).

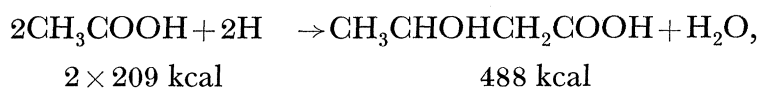
(g) *Fat as a fuel*

The results obtained with bees and flies agree with the classical idea that carbohydrate delivers the energy for muscular contractions (Hill & Meyerhof 1923). Since the days of Zuntz fat has been known to disappear during exercise (cf. Krogh & Lindhard 1920; Rapport & Ralli 1928; Marsh 1928), and it was therefore necessary to postulate a conversion of fat into carbohydrate (cf. Gemmill 1942), but in spite of many studies on the lipogenic origin of carbohydrates such a conversion has never been demonstrated with certainty in animals. This makes the postulated superiority of carbohydrate doubtful. However, there are certain features accompanying an intensive fat metabolism in mammals which have made it difficult to place carbohydrate and fat side by side. Thus the R.Q. of man generally increases with increasing intensity of work (Christensen & Hansen 1939*a*), and even an approaching hypoglycaemia is not always followed by a lowering (Christensen & Hansen 1939*b*), although in rare cases well-trained persons might endure heavy muscular work when not less than 90 % of the energy is derived from fat (Hansen 1942). Fat diet and the resulting low R.Q. is generally accompanied by a considerably decreased endurance (Christensen & Hansen 1939*c*), and, in the most thoroughly controlled experiments, the mechanical efficiency was found to decrease with increasing utilization of fat (Krogh & Lindhard 1920; Marsh & Murlin 1928), mechanical work demanding about 10 % more energy on fat than on carbohydrate. Investigations on isolated muscles (Hill & Meyerhof 1923) and on heart-lung preparations (Cruickshank & Startup 1933) showed that unless special precautions were taken the R.Q. was near to unity, and Buchwald & Cori (1931) as well as Gemmill (1940) were unable to demonstrate any decrease in the fat content of mammalian muscles when stimulated electrically *in situ*, whereas glycogen disappeared. In the latter investigations, however, it must be borne in mind that the amount of fat which might have been used could only constitute about  $\frac{1}{5000}$  of the total content of the body, and later investigations (see below) have shown that some muscles can make use of fat.

The evidence for considering fat as an inferior fuel used in case of emergency does not find support in the fact that it constitutes the main energy reserve in most animals and, moreover, some of the above effects are not necessarily associated with the combustion of fat as such. For example, training can increase the ability to work on a fat diet (Krogh & Lindhard 1920; Hansen 1942), and the ingestion of sugar need not increase the R.Q. of an exhausted person, although it immediately restored the ability to work, hypoglycaemia rather than the type of combustion causing the fatigue (Christensen & Hansen 1939*d*).



It is well established that proper functioning of the central nervous system depends on a high blood-sugar concentration, and glucose is therefore a necessary nutrient in the body as a whole. This does not imply, however, that fat is insufficient or of secondary importance for the working muscles. But in one respect carbohydrate has a great advantage over fat; it can be used under anaerobic conditions, whereas breakdown of fatty acids always demands oxygen. This might explain why the R.Q. increases with increasing intensity of work (Christensen & Hansen 1939*a*) or when less trained muscles are put into use (Hansen 1942). Concerning the lowered mechanical efficiency during fat combustion, no satisfactory explanation has yet been given. Recent investigations on the metabolism of fat have made it most probable that fatty acids are first converted into acetic acid which is further oxidized to carbon dioxide and water via the citric acid cycle (cf. Baldwin 1949). The main part of the energy contained in fat and carbohydrate will therefore be liberated through the same sequence of oxidations, ketone bodies being thought to be formed as a side product if acetates pass through the liver. If so, the direct combustion of fat is the original process, whereas the formation of ketone bodies is a secondary phenomenon. The relatively harmless ketone bodies may then be formed from acetates when an inadequate supply of oxygen prevents an immediate oxidation of acetic acid in the tissues or when the organism in question, for some reason or other, demands an increased concentration of easily diffusible energy sources in the circulating blood. The formation of  $\beta$ -hydroxybutyric acid from acetic acid demands energy according to the formula



If the energy of formation were irreversibly lost the oxidation of fatty acids via ketone bodies would deliver about 12% less energy than would a direct oxidation. According to the conditions the relative decrease in mechanical efficiency would therefore vary from a few to maximally 12%. This covers the diverging figures given by various authors (Krogh & Lindhard 1920; Marsh & Murlin 1928; Hansen 1942), and the assumed patterns of fat oxidation agree with Heilesen's (1947) experiments. Concerning isolated muscles, later investigations showed that the R.Q. could be considerably lower than unity (Himwich & Rose 1927; Meyerhof & Boyland 1931), and in the aglycaemic heart-lung preparation (R.Q. = 0.7) utilization of neutral fat and fatty acids have now been directly demonstrated (Cruickshank & McClure 1936; Barnes, MacKay, Moe & Visscher 1938; Cruickshank & Kosterlitz 1941). Blixenkron-Møller (1938) furthermore found that the stimulated hind limbs of eviscerated cats could utilize ketone bodies to such an extent that only 25% of the energy was derived from other sources even in the presence of exceptionally big amounts of glucose in the perfusing blood.

As a conclusion it can be said that investigations on heavy muscular work, on the intermediate metabolism of fat and carbohydrate, and on the fuels applied by isolated muscles all tend to show that, although carbohydrate is necessary for the central nervous system of vertebrates, fat need not be considered as inferior to carbohydrate as a fuel for well-oxygenated muscles, like the wing muscles of insects for instance. From this point of view the results obtained with *Schistocerca* are not surprising, and the prolonged and intensive combustion of fat would be difficult to understand if the type of metabolism had any serious

drawbacks. It has also previously been indicated that fat delivers energy for flight in the hemipteron *Eutettix tenellus* (Fulton & Romney 1940). Moreover, it was generally concluded that long-range migrations of small flying animals would only be possible if fat could be used, the hydration of stored glycogen making it about eight times heavier than isocaloric amounts of fat (Weis-Fogh 1952).

Fat and carbohydrate may therefore be of equal value when a steady state has been reached, but, as mentioned before, anaerobic breakdown of carbohydrate is an advantage which is not shared by fat, and one further advantage should be pointed out: it is reasonable to suggest that fuel can be mobilized more suddenly from dissolved glycogen than from hydrophobic fat droplets; both in man and in locusts carbohydrate is utilized in higher proportions when work starts than later on. In locusts this can hardly be caused by an inadequate initial supply of oxygen, as will be shown in a separate paper. 'Warming up' might thus take place quicker on carbohydrate than on fat. Flying locusts resemble heavy bombers, whereas the flight activity of bees and flies can be compared with that of fighters. This might explain why bees and flies demand carbohydrates and, in the course of evolution, have given up the ability to utilize fats.

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## REFERENCES

- Asmussen, E., Christensen, E. H. & Nielsen, M. 1939 Die O<sub>2</sub>-Aufnahme der ruhenden und der arbeitenden Skelettmuskeln. *Skand. Arch. Physiol.* **82**, 212.
- Baldwin, E. 1949 *Dynamic aspects of biochemistry*. Cambridge University Press.
- Barnes, R. H., MacKay, E. M., Moe, G. K. & Visscher, M. B. 1938 The utilization of  $\beta$  hydroxybutyric acid by the isolated mammalian heart and lung. *Amer. J. Physiol.* **123**, 272.
- Beutler, R. 1937 Über den Blutzucker der Bienen. *Z. vergl. Physiol.* **24**, 71.
- Blixenkroner-Møller, N. 1938 Über den Abbau von Ketonkörpern. *Hoppe-Seyl. Z.* **253**, 261.
- Blumenthal, R. 1927 A micro blood sugar method and the blood sugars of insects. *Science*, **65**, 617.
- Brand, T. v. 1936 A rapid working micro modification of Pflüger's glycogen method. *Skand. Arch. Physiol.* **75**, 195.
- Brodskis, B. 1944 La valeur alimentaire des sauterelles. *C.R. Soc. Sci. nat. Maroc.* no. 2, 9.

- Brodskis, B. & Rungs, C. 1944 Premières recherches sur les possibilités d'une détermination chimique des âges et des phases du criquet pèlerin (*Schistocerca gregaria* Forsk.). *C.R. Soc. Sci. nat. Maroc.* no. 2, 6.
- Brody, S. 1945 *Bioenergetics and growth*. New York: Reinhold.
- Brown, A. W. A. 1937 Studies on the excreta of a grasshopper (*Melanoplus bivittatus* Say.). *J. Exp. Biol.* **14**, 87.
- Buchwald, K. W. & Cori, C. F. 1931 Influence of repeated contractions of muscle on its lipid content. *Proc. Soc. Exp. Biol., N.Y.*, **28**, 737.
- Carpenter, T. M. 1939 *Tables, factors, and formulas for computing respiratory exchange and biological transformations of energy*. 3rd ed. Washington: Carnegie Institution, no. 303b.
- Chadwick, L. E. 1947 The respiratory quotient of *Drosophila* in flight. *Biol. Bull. Woods Hole*, **93**, 229.
- Chadwick, L. E. & Gilmour, D. 1940 Respiration during flight in *Drosophila repleta* Wollaston: the oxygen consumption considered in relation to the wing rate. *Physiol. Zool.* **13**, 398.
- Christensen, E. H. & Hansen, O. 1939a Respiratorischer Quotient und O<sub>2</sub>-Aufnahme. *Skand. Arch. Physiol.* **81**, 180.
- Christensen, E. H. & Hansen, O. 1939b Untersuchungen über die Verbrennungsvorgänge bei langdauernder schwerer Muskelarbeit. *Skand. Arch. Physiol.* **81**, 152.
- Christensen, E. H. & Hansen, O. 1939c Arbeitsfähigkeit und Ernährung. *Skand. Arch. Physiol.* **81**, 160.
- Christensen, E. H. & Hansen, O. 1939d Hypoglykämie, Arbeitsfähigkeit und Ermüdung. *Skand. Arch. Physiol.* **81**, 172.
- Cruickshank, E. W. H. & Kosterlitz, H. W. 1941 The utilization of fat by the aglycaemic mammalian heart. *J. Physiol.* **99**, 208.
- Cruickshank, E. W. H. & McClure, G. S. 1936 On the question on the utilization of amino acids and fat by the mammalian heart. *J. Physiol.* **86**, 1.
- Cruickshank, E. W. H. & Startup, C. W. 1933 The effect of insulin on the respiratory quotient, oxygen consumption, sugar utilization, and glycogen synthesis in the normal mammalian heart in hyper- and hypoglycaemia. *J. Physiol.* **77**, 365.
- Davis, R. A. & Fraenkel, G. 1940 The oxygen consumption of flies during flight. *J. Exp. Biol.* **17**, 402.
- Ellis, P. E. 1951 The marching behaviour of hoppers of the African Migratory Locust (*Locusta migratoria migratorioides* R. & F.) in the laboratory. *Anti-Locust Bull.* no. 7.
- Evans, A. C. 1939 The utilization of food by certain lepidopterous larvae. *Trans. R. Ent. Soc. Lond.* **89**, 13.
- Faure, J. C. 1932 The phases of locusts in South Africa. *Bull. Ent. Res.* **23**, 293.
- Federley, H. 1908 Einige Libellulidenwanderungen über die zoologische Station bei Tvärminne. *Acta Soc. Fauna Flora fenn.* **31**, no. 7.
- Fulton, R. A. & Romney, V. E. 1940 The chloroform-soluble components of beet leafhoppers as an indication of the distance they move in the spring. *J. Agric. Res.* **61**, 737.
- Gemmill, C. L. 1940 The effect of stimulation on the fat and carbohydrate contents of the gastrocnemius muscle in the phlorizinized rat. *Johns Hopk. Hosp. Bull.* **66**, 71.
- Gemmill, C. L. 1942 The fuel for muscular exercise. *Physiol. Rev.* **22**, 32.
- Giral, J., Giral, F. & Giral, M. L. 1946 Fats of insects: IV. Composition of the fat of *Melanoplus atlantis* Riley. *J. Biol. Chem.* **162**, 55.
- Groth-Petersen, E. 1940 *Grundlag for beregning af kostens næringsværdi*. Copenhagen: Gad.
- Gunn, D. L., Perry, F. C., Seymour, W. G., Telford, T. M., Wright, E. N. & Yeo, D. 1948 Behaviour of the Desert Locust (*Schistocerca gregaria* Forsk.) in Kenya in relation to aircraft spraying. *Anti-Locust Bull.* no. 3.
- Hagedorn, H. C., Halstrøm, F. & Jensen, B. N. 1946 Swift methods for determination of blood sugar by means of potassium ferricyanide. *Rep. Steno Mem. Hosp.* **1**, 29.

- Hansen, O. 1942 *Undersøgelser over stofskifteprocesserne ved muskelarbejde*. Thesis. Copenhagen: S. L. Möller.
- Harman, J. W. 1950 Studies on mitochondria. II. The structure of mitochondria in relation to enzymatic activity. *Exp. Cell. Res.* **1**, 394.
- Heilesen, B. 1947 Investigations concerning the utilization of ketone bodies during muscular exercise. *Acta physiol. Scand.* **13**, 181.
- Hemmingsen, A. M. 1924 The blood sugar of some invertebrates. *Skand. Arch. Physiol.* **45**, 204.
- Hilditch, T. P. 1947 *The chemical constitution of natural fats*, 2nd ed. London: Chapman and Hall.
- Hill, A. V. & Meyerhof, O. 1923 Über die Vorgänge bei der Muskelkontraktion. *Ergbn. Physiol.* **22**, 299.
- Himwich, H. E. & Rose, M. I. 1927 The respiratory quotient of exercising muscle. *Amer. J. Physiol.* **81**, 485.
- Jongbloed, J. & Wiersma, C. A. G. 1935 Der Stoffwechsel der Honigbiene während des Fliegens. *Z. vergl. Physiol.* **21**, 519.
- Katz, L. N. 1932 Observations on the external work of the isolated turtle heart. *Amer. J. Physiol.* **99**, 579.
- Kennedy, J. S. 1951 The migration of the Desert Locust (*Schistocerca gregaria* Forsk.). *Phil. Trans. B*, **235**, 163.
- Kennedy, E. P. & Lehninger, A. L. 1948 Intracellular structures and the fatty acid oxydase system of rat liver. *J. Biol. Chem.* **172**, 847.
- Krogh, A. 1948 Determination of temperature and heat production in insects. *Z. vergl. Physiol.* **31**, 274.
- Krogh, A. & Lindhard, J. 1920 The relative value of fat and carbohydrate as sources of muscular energy. *Biochem. J.* **14**, 290.
- Krogh, A. & Weis-Fogh, T. 1951 The respiratory exchange of the Desert Locust (*Schistocerca gregaria*) before, during and after flight. *J. Exp. Biol.* **28**, 344.
- Krogh, A. & Weis-Fogh, T. 1952 A roundabout for studying sustained flight of locusts. *J. Exp. Biol.* (in preparation).
- Larsen, A. 1950 Guldsmedetræk over Danmark. *Flora og Fauna*, **56**, 105.
- Magnan, A. 1934 *Le vol des insectes*. Paris: Hermann et Cie.
- Marsh, M. E. 1928 The character of energy metabolism during work. *J. Nutrit.* **1**, 57.
- Marsh, M. E. & Murlin, J. R. 1928 Muscular efficiency on high carbohydrate and high fat diets. *J. Nutrit.* **1**, 105.
- Meyerhof, O. & Boyland, E. 1931 Über den Atmungsvorgang jodessigsäurevergifteter Muskeln. *Biochem. Z.* **237**, 406.
- Nordman, A. F. 1935 Über Wanderungen der *Libellula quadrimaculata* L. bei der zoologischen Station Tvärminne in S.-Finnland im Juni 1932 und 1933. *Notul. Ent.* **15**, 1.
- Pearson, O. P. 1950 The metabolism of humming birds. *Condor*, **52**, 145.
- Pfeiffer, I. W. 1945 Effect of the corpora allata on the metabolism of adult female grasshoppers. *J. Exp. Zool.* **99**, 183.
- Raffy, A. & Portier, P. 1931 Intensité des échanges respiratoires pendant le vol chez les Lépidoptères. *C.R. Soc. Biol., Paris*, **108**, 1062.
- Rainey, R. C. & Waloff, Z. 1951 Flying locusts and convection currents. *Anti-Locust Bull.* no. 9, 51.
- Rapport, D. & Ralli, E. P. 1928 The nature of the foodstuffs oxidized to provide energy in muscular exercise. *Amer. J. Physiol.* **83**, 450.
- Rasmussen, H. J. 1941 *Fodringslære*, 9th ed. Copenhagen: Bang.
- Ribbands, C. R. 1950 Change in the behaviour of honey-bees following their recovery from anaesthesia. *J. Exp. Biol.* **27**, 302.
- Schneider, W. C. 1948 Intracellular distribution of enzymes. III. The oxidation of octanoic acid by rat liver fractions. *J. Biol. Chem.* **176**, 259.

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- Schoendorff, B. 1903 Über den Maximalwerth des Gesammtglykogengehalts von Hunden. *Pflüg. Arch. ges. Physiol.* **99**, 191.
- Sotavalta, O. 1947 The flight-tone (wing-stroke frequency) of insects. *Acta Ent. Fennica*, **4**, 1.
- Terroine, E. F. 1920 Contribution à la connaissance de la physiologie des substances grasses et lipoidiques. *Ann. sci. nat. (Zool.)* (10), **4**, 5.
- Timon-David, J. 1930 Recherches sur les matières grasses des insectes. *Ann. Fac. Sci. Marseille*, (2), **4**, 29.
- Uvarov, B. P. 1928 *Locusts and grasshoppers*. London: Imp. Bur. Ent.
- Uvarov, B. P. 1948 Recent advances in acridology: anatomy and physiology of Acrididae. *Anti-Locust Bull.* no. 1.
- Waloff, Z. 1946 A long-range migration of the Desert Locust from southern Morocco to Portugal, with an analysis of concurrent weather conditions. *Proc. R. Ent. Soc. Lond. (A)*, **21**, 81.
- Waloff, Z. & Rainey, R. C. 1951 Field studies on factors affecting the displacements of Desert Locust swarms in eastern Africa. *Anti-Locust Bull.* no. 9, 1.
- Watanabe, M. I. & Williams, C. M. 1951 Mitochondria in the flight muscles of insects. I. Chemical composition and enzymatic content. *J. Gen. Physiol.* **34**, 675.
- Weis-Fogh, T. 1952 Weight economy of flying insects. *Proc. 9th Int. Congr. Ent. Amsterdam*, 1951 (in preparation).
- Wigglesworth, V. B. 1949 The utilization of reserve substances in *Drosophila* during flight. *J. Exp. Biol.* **26**, 150.
- Wigglesworth, V. B. 1950 *The principles of insect physiology*, 4th ed. London: Methuen and Co. Ltd.
- Williams, C. M., Barness, L. A. & Sawyer, W. H. 1943 The utilization of glycogen by flies during flight and some aspects of the physiological ageing of *Drosophila*. *Biol. Bull. Woods Hole*, **84**, 263.
- Zeuthen, E. 1941 Cited by Krogh, A. *The comparative physiology of respiratory mechanisms*, p. 129. Philadelphia: University Pennsylvania Press.
- Zeuthen, E. 1947 Body size and metabolic rate in the animal kingdom. *C.R. Lab. Carlsberg*, **26**, 17.