J. exp. Biol. **118**, *313–326 (1985)*
Printed in Great Britain © *The Company of Biologists Limited 1985*

THE DEVELOPMENT OF THE LOCUST JUMPING MECHANISM

I. ALLOMETRIC GROWTH AND ITS EFFECT ON JUMPING PERFORMANCE

BY JULIE M. GABRIEL*
Department of Zoology, South Parks Road, Oxford, England

Accepted 2 April 1985

SUMMARY

1. The jump range of locusts of all instars varies throughout an instar, reaching a peak at apolysis in hoppers, and about 3 weeks after the final moult in adults.

2. Mature adult locusts have an escape jump range three times that of young hoppers.

3. During a period of *repeated* jumping, mature adults have an average jump range three times that of the hoppers.

4. Allometric growth of the metathoracic leg occurs during development, and accounts for 25 % of the increase in range between the fourth instar and adult, the remaining increment being due to absolute size increase.

5. The allometric changes do not, however, affect the mechanics of the femoro-tibial joint. The extensor apodeme to tarsus lever ratio remains at 27:1 in the fourth, fifth and adult stages. The extension of the joint would be expected to follow a similar pattern in the fourth instar and adult stages.

6. The change in form of the metathoracic leg of the locust also means that the adult femur accommodates more muscle, i.e. 6·3 % of the total body weight in the adult male, as opposed to 4·3 % in the fourth instar male. Therefore relatively more force and energy may be available for use in a jump.

7. The lengthening of the semilunar processes may be expected to have an effect on the energy storage capacity of the leg.

8. In an escape jump, all instars use the same specific power output, which is more than the published figures for maximum specific power output ($250\,\mathrm{W\,kg^{-1}}$, Weis-Fogh & Alexander, 1977, and $860\,\mathrm{W\,kg^{-1}}$, Pennycuick & Parker, 1966). This suggest that energy storage is necessary in locust hoppers.

---

*Present address: Department of Zoology, Downing Street, Cambridge, England.

Key words: Locust, allometry, jumping.

INTRODUCTION

The hop or jump is a relatively common form of locomotion. The jumping performance of several species has been investigated in detail, e.g. the bushbaby (Hall-Craggs, 1965), the click beetle (Evans, 1972, 1973) and the locust. Several aspects of the escape jump of the adult locust have been investigated, e.g. the energy storage system (Brown, 1967; Bennet-Clark, 1975), the motor programme (Heitler & Burrows, 1977*a*; Pflüger & Burrows, 1978), and the neural circuits (Heitler & Burrows, 1977*b*; Pearson, Heitler & Steeves, 1980; Pearson & Goodman, 1981; Steeves & Pearson, 1982). The jump of the immature locust (the hopper) has, however, been neglected.

Small jumping animals have high efficiencies only at short jump ranges (Bennet-Clark & Alder, 1979). In migration, therefore, locust hoppers would be expected to produce many short hops, rather than fewer long ones. This 'marching' behaviour has been observed on many occasions both in the field, and in the laboratory (Ellis, 1951). A locust (hopper or adult) jumping to escape predators has different requirements. If it does not jump far enough or fast enough it will be captured. Thus it is worth investing a large amount of energy in a single jump to evade a predator. In addition, the adult locust uses jumping as a means of reaching take-off velocity for flight.

In the growth of an individual, there may be changes in body proportions with either size or age, and this allometric growth would be expected to affect locomotory performance. For example, relatively longer legs would be advantageous in jumping animals, as this would increase acceleration distance, so decreasing forces due to acceleration (Bennet-Clark, 1977). Longer legs would also reduce the power output necessary for a jump of a particular length. In addition, the mechanics of the metathoracic femoro-tibial joint may be affected by allometric growth, which would in turn affect locomotory performance. Several studies have examined the mechanics of the femoro-tibial joint in the adult locust, e.g. Heitler (1974, 1977) and Bennet-Clark (1975).

Bennet-Clark (1977) cited unpublished work by McGavin & Bennet-Clark indicating that escape jump range varies with age in the locust, *Schistocerca gregaria*. In this paper the size and form of locusts of different instars are investigated, and their escape jump range is considered. The dimensions of the metathoracic leg are studied in detail, and various aspects of the mechanics of the joint, which may be affected by allometric growth, are examined. From these data, the proportion of change in performance due to each variable can be calculated.

MATERIALS AND METHODS

Male desert locusts (*Schistocerca gregaria* Forskål) of all instars were used in these experiments. Animals were obtained from crowded laboratory cultures, maintained as recommended by Hunter-Jones (1961). The culture room and experimental area were kept at a temperature of 29 ± 1 °C. Experimental animals were removed from the culture at ecdysis, and were transferred to cages marked with the date, to provide a supply of animals of known age within each instar.

For the investigation of allometric growth, animals of appropriate age were weighed before use. To compare the dimensions of animals, it is necessary to relate them to a standard dimension. In this study the standard dimension of $\text{mass}^{1/3}$ at a characteristic time has been used. Apolysis occurs during the period of peak jumping performance (see below), and is therefore a convenient characteristic time. A relative length (or *k* value) is defined as an absolute length divided by $\text{mass}^{1/3}$ at apolysis. If the animals are geometrically similar, one would expect the resulting values to be equal in different instars. A Watson Bactil microscope was fitted with a curtain micrometer eyepiece for measurement of body dimensions.

Using the method of Bennet-Clark (1975), jumping performance was measured on most days of each instar up to the 21st day of the adult stage. Locusts were placed on a low platform at the centre of an arena marked with concentric lines at 0·1 m radii out to 1·2 m. Each locust was induced to jump 10 times, and was allowed 5-min rest periods between jumps. Range was estimated to the nearest 50 mm. The longest jump recorded for each individual was taken to be its maximum escape jump range, and was used in subsequent calculations. Hoppers usually jumped immediately after release into the arena. Adult locusts, however, required some stimulation to jump, e.g. a slight electric shock produced by the jumping platform (Bennet-Clark, 1975) or prodding with a pencil. The mass of the animal, the mass of each metathoracic extensor tibiae muscle and the length of each metathoracic femur were also measured.

The lever ratio between the extensor apodeme and the tibio-tarsal joint was determined from the moment arm of the extensor apodeme and the tibia length. For the measurement of flexor to extensor mechanical advantage, metathoracic legs (right or left) from adult and fourth instar male locusts, at the age of peak jumping performance, were used. Whole, fresh legs were fixed horizontally onto a balsa wood stand. The femur proximal to Heitler's lump (Heitler, 1974) was dissected to expose the flexor and extensor apodemes. Washington Dl force transducers (0–50 g range), mounted on micromanipulators, were attached to the apodemes, with the direction of pull adjusted to be as near natural as possible. Forces were recorded on a Washington 400MD2C pen recorder. A circular protractor was fitted to the draw-tube of the microscope which could then be used to measure angles of joint extension. The flexor-to-extensor mechanical advantage at different angles could then be found from the ratio of the forces required to hold the joint at each angle.

Photographs by Brown (1963) indicate an angle of about 130° between femur and tibia at take-off so the acceleration distance, s, for a locust is given by:

$$s = 2 \times (\text{femur length}) \times \sin 65^\circ .$$

Take-off velocity, acceleration, peak power output required in the take-off phase and specific power (in watts per kilogram of extensor muscle) were found using standard projectile theory (e.g. Bennet-Clark, 1975; Gabriel, 1984).

Jumping performance over a 10-min period was also investigated. This 'endurance jumping' was intended to show the ability of the jumping muscle to provide energy over a long time period, but not to simulate migration, as adult locusts migrate by flying and hoppers by marching (Ellis, 1951). A grid was constructed on a large sheet of paper, with lines in alternating colours at 0·1-m intervals. Part of the sheet also had grid lines marked every 0·02 m; animals producing short jumps were encouraged to stay in this area. Animals of known age were placed on the grid and forced to jump continuously for a 10-min period. The range of each jump was recorded on cassette tape for later analysis.

For all measurements, means, standard deviations and number of observations are quoted as appropriate. One-way analysis of variance, followed by significance tests on the means, and least squares regression analysis were used.

RESULTS

Jumping performance

Within each instar, there is some variation in escape jump range. For all hoppers, the day of peak performance occurs at approximately the time of apolysis, as shown by the condition of the cuticle on dissection. Adult jump range increases with time from the imaginal moult. Performance 21 days after the moult was taken as the peak, as the animals are sexually mature at this time, and there is very little change in their jumping performance after this stage.

Fig. 1 shows escape jump range for day 0 (the day of hatching or moulting, as appropriate), and for the day of peak performance. In each instar, the day 0 range is much lower than that of the peak day. The difference increases at the fifth instar and adult stages. On day 0, the jumping range of the fifth instar and adult animals is not significantly superior to that of the young hoppers.

The maximum range for the first four instars is similar at just under 0·3 m, but fifth instar and adult locusts jump substantially further at 0·5 m and 0·9 m, respectively (Fig. 1). Thus an adult can jump three times as far as a fourth instar animal. The remainder of this paper seeks an explanation for this large increase in range.

When forced to jump over a long period the adult locust produces fewer, longer jumps than the hoppers, but it jumps a greater total distance (Table 1). In the

Table 1. *Peak jumping performance of locusts of different ages over a 10-min period*

	Number		Average range of single jump (m)		Total range (m)	
Instar	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
4	248	81	0·137	0·026	26·7	3·9
5	280	60	0·107	0·022	29·0	2·5
Adult	104	35	0·371	0·112	35·9	8·6

N = five locusts in each case.

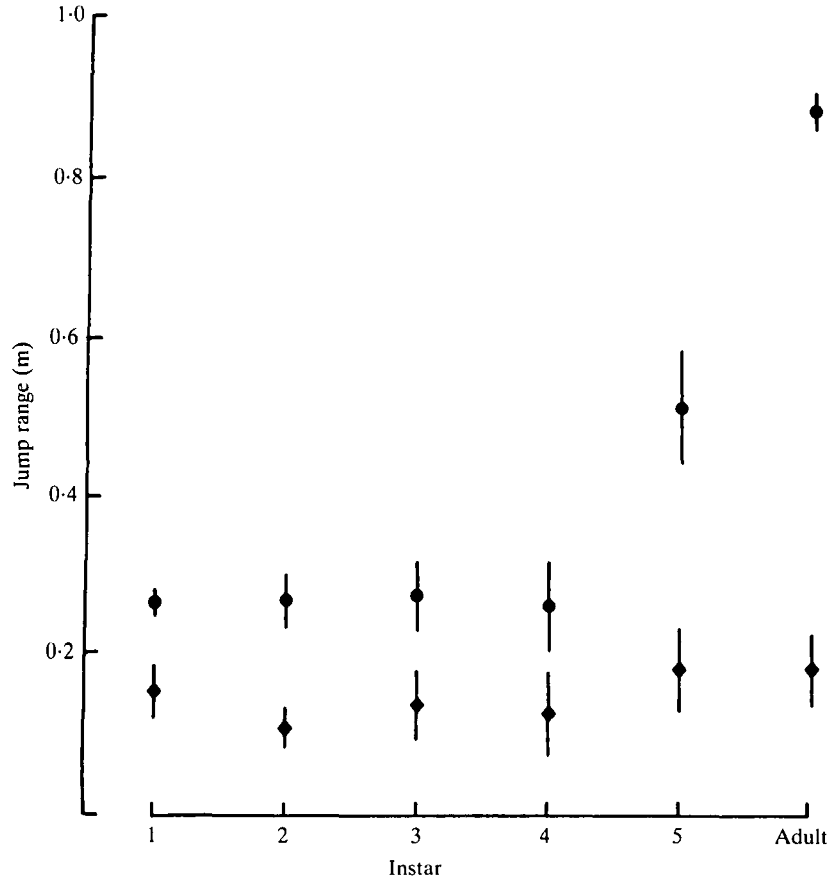

Fig. 1. Means and standard deviations of escape jump ranges for locusts of all instars. Performance on the first day of the instar (◆), and on the peak performance day (●). $N=5$.

comparison of escape jump performance, the age within an instar is of great importance. In endurance jumping, both fourth instar and adult animals produce shorter, but many more, jumps on the day of the moult (Table 2). In addition, they may jump a slightly shorter total distance.

Allometric growth

Between-instar variation

Fourth instars and adults were compared in detail for this study. Most parts of the body are geometrically similar; dimensions such as body length, pronotum length, head capsule width and prothoracic leg length show isometry. There is some change in shape of the pronotum during the nymphal phase of development. Initially, the pronotum is oval in cross-section, but by the fourth instar it has become triangular, and in the adult stage it is almost rectangular. The dorsum of the pronotum expands relative to the rest of the pronotum between the fourth instar and adult stages to accommodate the increasing mass of the flight muscles.

Table 2. *The jumping performance of locusts of different ages within the fourth instar and adult stages over a 10-min period*

Age Instar (days)	Number $\bar{x}$	Number S.D.	Average range of single jump (m) $\bar{x}$	Average range of single jump (m) S.D.	Total range (m) $\bar{x}$	Total range (m) S.D.
Fourth						
0	446	218	0·050	0·016	19·7	6·6
2	300	37	0·100	0·017	29·6	3·6
4	302	90	0·098	0·027	27·8	5·6
6	248	81	0·137	0·026	26·7	3·9
Adult						
0	352	54	0·074	0·017	25·5	4·3
7	151	59	0·251	0·086	34·2	5·9
14	141	43	0·310	0·096	40·6	6·4
≥21	104	35	0·371	0·112	35·9	8·6

N = five locusts in each case.

Significant changes in proportion are most evident for the legs, however, and in particular for the metathoracic (jumping) legs, whose overall shape is slightly different from that of the hoppers (Fig. 2). Height and width of the leg were measured at three sections (marked on Fig. 2). The metathoracic leg of the adult locust is proportionately longer and at some sections (1 and 3) higher and wider than the fourth instar leg. These differences are highly significant, and may be of importance to the jumping performance. The means and standard deviations of

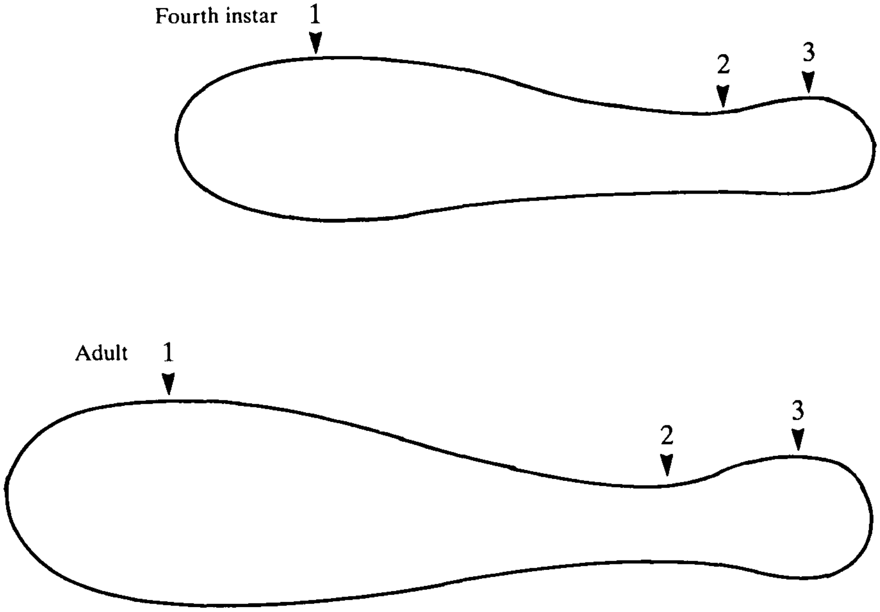

Fig. 2. The shapes of the metathoracic femora of fourth instar and adult locusts, showing the sections at which width and height measurements were made.

various dimensions divided by mass$^{1/3}$ are given in Table 3. Fig. 3 show metathoracic femur length and height (at section 1) for all instars, presented as the value of length divided by mass$^{1/3}$. Clearly, femur height is geometrically similar for the first four instars and then increases disproportionately. Femur length shows a tendency to increase slightly throughout life but this is more marked between the fifth instar and adult stages. The adult locust has larger extensor tibiae muscles in proportion to its total mass than the fourth instar. The extensor muscles make up 4·3% of the mass of the fourth instar and 6·3 % of the mass of the adult (Table 4), so relatively more force and energy may be available to the adult for use in a jump.

The metathoracic tibia and tarsus also show some change between the fourth and adult stages (Table 3). In the adult, the tibia is proportionately longer (thus increasing acceleration distance) and higher, though not wider. The tarsus is proportionately longer, as are the heel spines – this may allow increased force on the ground at take-off for a jump.

Prior to an escape jump, the adult locust stores mechanical energy in the extensor apodeme and semilunar processes (Bennet-Clark, 1975). The semilunar processes can be seen from external dimensions to be proportionately both longer and deeper in the adult stage. These changes in external dimensions might be expected to affect the energy storage properties.

Table 3. *Means and standard deviations of various body dimensions divided by mass*$^{1/3}$

Dimension	Fourth instar ($N=5$) Mean	S.D.	Adult ($N=5$) Mean	S.D.	*P*
Body length	0·3805	0·0384	0·3951	0·0196	NS
Wing length	0·0581	0·0028	0·3877	0·0089	<0·001*
Mesothoracic leg:					
femur length	0·0514	0·0025	0·0594	0·0030	<0·005*
tibia length	0·0642	0·0038	0·0685	0·0056	NS
tarsal length	0·0420	0·0020	0·0462	0·0024	<0·025
Metathoracic leg:					
femur length	0·1361	0·0099	0·1713	0·0076	<0·001
femur height 1	0·0297	0·0016	0·0385	0·0012	<0·001
femur width 1	0·0188	0·0009	0·0217	0·0007	<0·001
femur height 2	0·0164	0·0014	0·0153	0·0009	NS
femur width 2	0·0138	0·0003	0·0135	0·0004	NS
femur height 3	0·0187	0·0007	0·0232	0·0002	<0·01*
femur width 3	0·0142	0·0008	0·0190	0·0009	<0·001
tibia length	0·1373	0·0079	0·1603	0·0065	<0·001
tibia height	0·0093	0·0004	0·0104	0·0006	<0·02
tibia width	0·0069	0·0003	0·0066	0·0003	NS
tarsal length	0·0520	0·0031	0·0595	0·0039	<0·01
heel spine length	0·0142	0·0023	0·0175	0·0017	<0·05
Semilunar process:					
length	0·0165	0·0010	0·0228	0·0026	<0·001
height (mid-point)	0·0044	0·0004	0·0066	0·0005	<0·001
height of fold	0·0013	0·0002	0·0018	0·0003	<0·025

Values are referred to as *k* values in the text, and are given in mkg$^{-1/3}$.
Level of significance as found by Student's *t*-test is shown in the last column, NS = not significant.
*Level of significance as found by the *d*-test for small samples (variances not assumed equal).

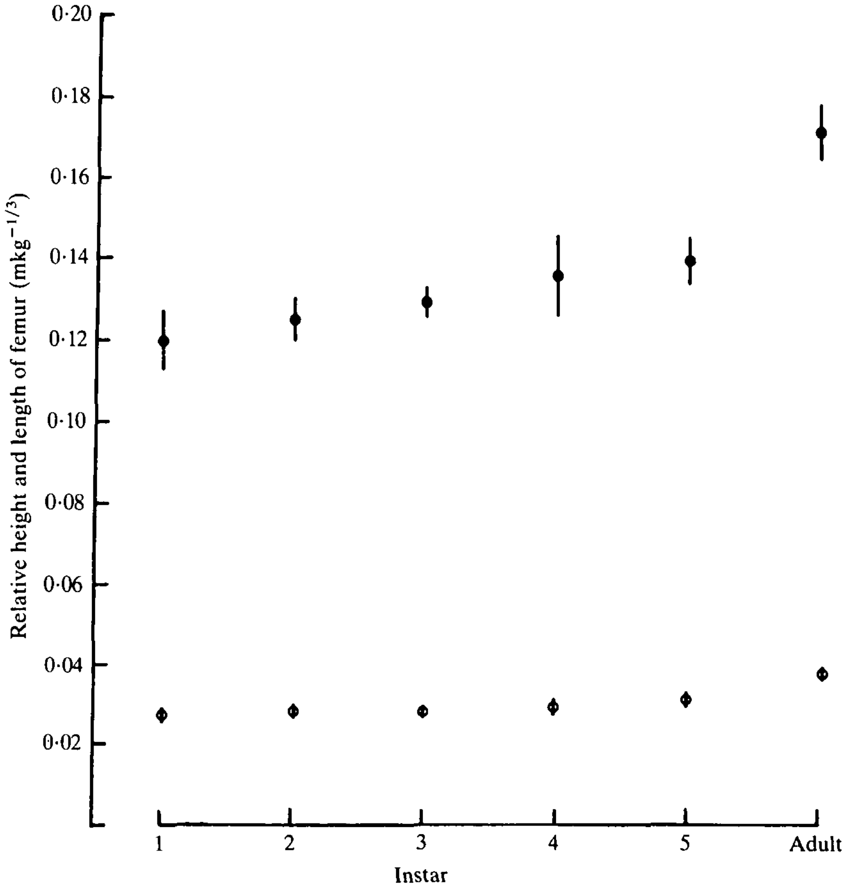

Fig. 3. The means and standard deviations for the values of femur length (●) and height at section 1 (○), all divided by mass$^{1/3}$. $N = 5$.

Table 4. *The total body mass, metathoracic extensor tibiae mass (both legs) and the proportions of metathoracic extensor tibiae muscle to body mass, in different instars*

	Body mass		Extensor mass		Extensor/body (*n*)	
Instar	Mean	S.D.	Mean	S.D.	Mean	S.D.
1	0·0310	0·0035	0·00189	0·00029	0·061	0·005
2	0·0799	0·0172	0·00368	0·00050	0·047	0·008
3	0·1832	0·0411	0·00901	0·00090	0·050	0·007
4	0·3061	0·0403	0·01343	0·00279	0·043	0·004
5	1·0062	0·0854	0·05492	0·00518	0·055	0·005
Adult	1·9923	0·2596	0·12491	0·01748	0·063	0·002

F-ratio for the extensor/body proportion $= 9{\cdot}92$ with 5,24 degrees of freedom, $P < 0{\cdot}001$.

Student's *t*-test (between consecutive instars) gave significant differences between the first and second instars ($t = 3{\cdot}978$, 24 df, $P < 0{\cdot}001$), the fourth and fifth instars ($t = 3{\cdot}306$, $P < 0{\cdot}01$) and the fifth instar and adult animals ($t = 2{\cdot}340$, $P < 0{\cdot}05$).

Mass is given in grams.

$N =$ five locusts in each case.

Within-instar variation

As mass increases during each instar, but lengths are fixed, the values of length divided by mass$^{1/3}$ must also change. Table 5 shows the *k* values for metathoracic femur length in adults of different ages.

Joint mechanics

Extensor apodeme to tarsus lever ratio

Values for tibia length and moment arm (a) of the extensor apodeme for the fourth, fifth and adult instars are shown in Table 6. The moment arm increases, as does the tibia length. Values for lever ratio (r = tibia / a) are also shown in Table 6, and fourth, fifth and adult instars each have an extensor apodeme to tarsus lever ratio of 27: 1.

Flexor to extensor mechanical advantage

At very large angles of extension (greater than 140 °), the mechanical advantage is difficult to measure (particularly in the fourth instar animals) because the leg is liable to break due to large forces on the extensor apodeme. Also, at extreme angles the angle of pull of the transducers become more critical, and leads to greater variability in the results. Data points were not collected with the leg fully flexed, because the locking mechanism of the leg would normally be in operation at this angle. Hence mechanical advantages at intermediate angles only are given

Table 5. *The mean and standard deviation values of* k *for metathoracic femur length, in adults of different ages*

Age (days)	Mean	S.D.
1	19·9	0·4
7	18·7	0·7
14	17·1	0·6
Mature	18·0	0·4

One-way analysis of variance gave F = 24·04, df = 3,16, which is significant at the $P < 0{\cdot}001$ level. Student's *t*-test between the means of the 1-day-old and 7-day-old animals gave $t = 3{\cdot}690$, 16 df, $P < 0{\cdot}002$. N = five locusts in each case.

Table 6. *The means and standard deviations for tibia length and moment arm (a) of the extensor apodeme (in millimetres)*

	Tibia		a		r	
Instar	Mean	S.D.	Mean	S.D.	Mean	S.D.
4	10·66	0·59	0·40	0·02	26·9	1·2
5	16·04	0·55	0·58	0·02	27·6	1·2
Adult	20·04	1·17	0·74	0·05	27·0	0·9

F-ratio for the lever ratio = 1·187, df = 2,27, so there is no significiant difference.
Values for the lever ratio (r = tibia / a) are also given. $N = 10$ locusts in each case.

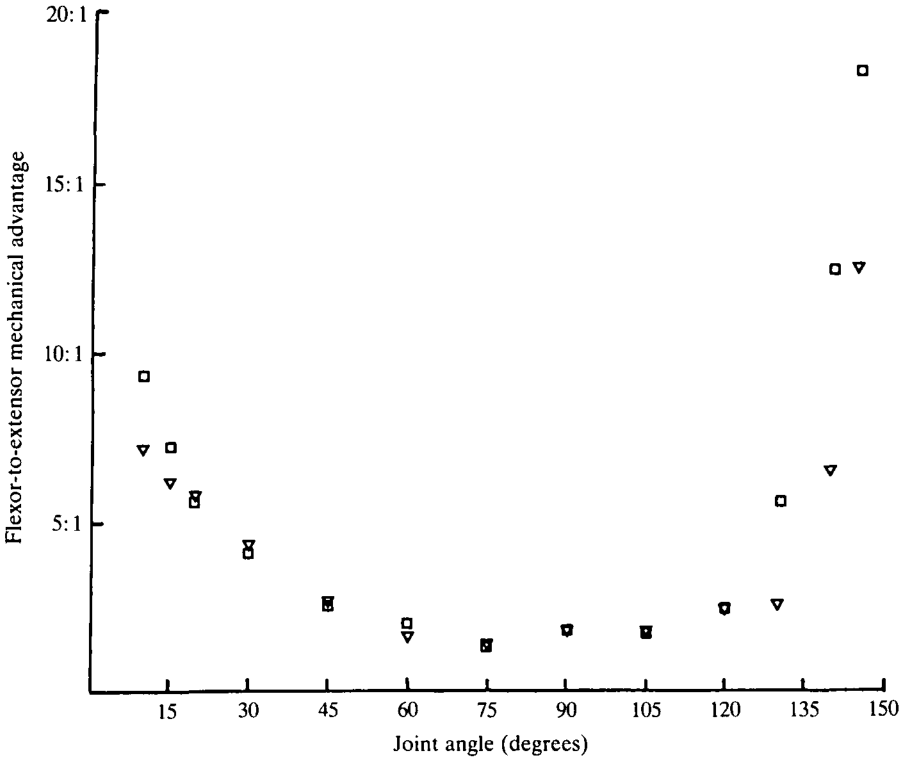

Fig. 4. The flexor-to-extensor mechanical advantage at different angles of extension of the femoro-tibial joint in fourth instar (▽) and adult locusts (□). $N=5$.

in Fig. 4. The fourth instars and adults follow the same pattern, with high mechanical advantage at the extreme joint angles and low mechanical advantage in the middle range, as would be expected from the structure of the joint. In both cases, the mechanical advantage of the extensor apodeme should vary sinusoidally with joint angle; but in the adult stage, Heitler's lump is known to act as a pulley for the flexor apodeme (Heitler, 1974), so that increasing the angle of extension decreases the effective mechanical advantage of the flexor apodeme. This also appears to be true in fourth instars.

DISCUSSION

If only the *energy* requirements of jumping animals are considered, it appears that similar animals of any size should have the same jump range (Maynard Smith, 1968; Bennet-Clark, 1977). However, Bennet-Clark (1967, 1975) and Bennet-Clark & Lucey (1967) have shown that, for small animals, the *power* requirements for long jumps cannot be met by direct muscle action. Therefore *power* availability may be a limiting factor in jumping.

In the comparison of locusts of different instars, superficially similar animals are being examined. As has been shown in this paper, they do not always have the same maximum jump range, although at the start of the instar their range is similar. Between each moult and subsequent apolysis, the escape jump range increases. This increase is more marked in the fifth instar and adult stages. There are several possibilities to account for the change in jumping performance in fifth instar and adult animals. These include: (a) air resistance, (b) the effect of scale, (c) allometric growth, (d) a change in the structure of the femoro-tibial joint and (e) changes in the properties of the muscular or energy storage systems. The effect of air resistance is small in all instars. It amounts to a reduction in jump distance of probably less than 10 % in fourth instar locusts (calculated from Fig. 3, p. 110 of Bennet-Clark & Alder, 1979). This does not account for the difference in jumping performance. The effect of scale has also been investigated elsewhere (Bennet-Clark 1977; Gabriel, 1984). The effect of relative proportions and joint mechanics on expected jumping performance are considered below.

Duarte (1938) investigated the growth of solitary and gregarious phases of the migratory locust, *Locusta migratoria migratorioides* (R. & F.). He applied the allometric equation to the growth of *Locusta*, using the mesothoracic femur as a reference dimension, and showed that the metathoracic femur exhibited isometric growth. However, at least in *Schistocerca*, the mesothoracic femur cannot be taken as an unbiased reference dimension. Growth of the meso- and metathoracic legs in *Schistocerca* shows positive allometry, not isometry, with respect to the whole animal. Additionally, the moment arm of the metathoracic extensor tibiae muscle shows positive allometric growth in the same way as the tibia length. This results in a constant extensor apodeme to tarsus lever ratio between the fourth instar and adult stages. The femoro-tibial joints of the fourth instar and adult are morphologically similar. The results for the flexor to extensor apodeme mechanical advantage for both fourth instar and for adult locusts given here follow the same pattern as those presented by Heitler (1974) for the adult locust.

Locusts, then, do not maintain geometric similarity during development. As femur length increases relative to size throughout the life of the locust, and particularly at the adult stage, this might explain the increased jumping performance. To test this hypothesis, power required in a jump can be related to size by the equation:

$$\mathrm{d} = (3{\cdot}62 k n \mathrm{m}^{1/3} \mathrm{P_m})^{2/3} / g,$$

where d = range, k = relative femur length (Table 3), n = proportion of body mass given over to extensor muscle (see Table 4), m = body mass (Table 4), $\mathrm{P_m}$ = specific power output required from the extensor muscle and g = acceleration due to gravity, $9{\cdot}81\ \mathrm{m\,s^{-2}}$. The derivation of this equation is given by Gabriel (1984).

If all other values are kept constant, then range is proportional to $k^{2/3}$. The increase of k from 0·136 to 0·171 between the fourth instar and adult stages will only increase the distance jumped by 16 %. This does not account for the difference in jumping performance. If the proportion of body mass given over to jumping muscle is *also* taken into account (i.e. $n = 0{\cdot}043$ in the fourth instar and

0·063 in the adult), jump distance increases by 50·3 %. Thus an adult locust with the same body mass as a fourth instar locust would be expected to jump 0·45 m. So changes in leg length and muscle mass account for 25 % of the difference in jumping performance between the fourth instar and adult stages.

The remainder of the increase is due to the increase in absolute size. A fourth instar locust has a mass of 0·3–0·5 g, while an adult male has a mass of 1·5–2·0 g, with jump range scaling as mass$^{2/9}$. Fig. 5 shows the expected ranges for all instars, using actual values of *k* and *n*, at different levels of specific power output. For the peak range of each instar, approximately the same specific power output is required. The maximum specific power output measured for adult locust extensor tibiae muscle, under repeated stimulation, of 450 W kg^{-1} (Bennet-Clark, 1975) is also shown. It can be seen that all instars produce more power in an escape jump than should be possible. Bennet-Clark (1975) showed that, in order to produce sufficient power, adults store energy in cuticular springs prior to an escape jump. The results presented here suggest that energy storage is also necessary in locust hoppers.

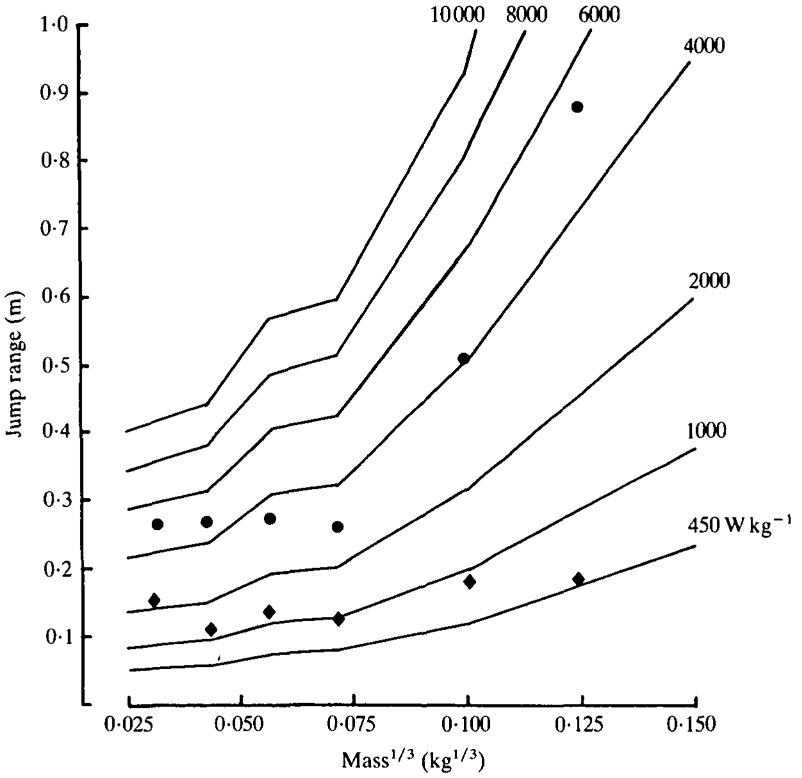

Fig. 5. The expected jump range of locusts of different size and shape, using various values of specific power as shown, and values of *k* and *n* measured for each instar. The actual jump ranges of each instar are also shown, day 0 (◆) and day of peak performance (●).

Allometric growth of the metathoracic leg results in a change in shape of the semilunar processes, which are known to form part of the energy storage system used by the adult locust (Bennet-Clark, 1975). Shape change would probably affect the energy storage capacity of the system. This is discussed further in the following paper, in relation to measurements of semilunar process stiffness.

A further effect of allometric growth is that the mechanical strength of the system will be affected. For example, the height (dorsal to ventral) of the tibia increases disproportionately in the adult stage, which probably increases the resistance of the tibia to bending and Euler buckling. It would, however, tend to increase the probability of local buckling (Currey, 1967). A disproportionate increase in tibial cuticle thickness, particularly dorsal and ventral, would be needed to counteract this effect.

The structure of the femoro-tibial joint in the fourth instar and adult stages has been shown here to be essentially the same. The extension of the joint would, therefore, be expected to follow a similar pattern in these instars. At low angles of extension, the flexor muscle has a high mechanical advantage over the extensor, so a small flexor muscle can hold the leg flexed against the action of the larger extensor muscle (Heitler, 1974). Thus energy storage can occur. The pattern of flexor-to-extensor apodeme mechanical advantage would favour the exertion of the greatest forces near the middle phase of leg extension in both instars.

Variation within instars

Mass varies within an instar, but leg length does not, so the relative femur length varies within an instar. A change in k should not, however, give rise to any change in jump range within an instar, because the increase in mass$^{1/3}$ would cancel out the effect of the change in k. Thus changes in jump range must be due to another cause.

Fig. 5 also shows the jump range of first day animals of each instar, superimposed on the expected range for each instar, using real values of k and n, and various values of specific power. Even close to the beginning of each instar, the animals appear to produce more power than should be possible. It has been shown previously that all instars must store energy in order to produce sufficient power for their maximum range jumps. On the first day of the instar either the amount of energy storage must be much less or there must be a change in the properties of the jumping muscle.

When the jumping performance over a long time period is examined (Table 1, 2), adults are again found to produce longer individual jumps. They also produce far fewer jumps than the hoppers. Although there appears to be a trend for increased total distance, it is not statistically significant. If tested on the day of the moult, both fourth instar and adult animals are capable of short jumps only. This indicates that the ability to produce long jumps develops after the moult, probably as a result of a change in the properties of the cuticular energy stores rather than the muscle.

REFERENCES

BENNET-CLARK, H. C. (1967). How fleas jump. *New Scientist* **35**, 484–487.

BENNET-CLARK, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. exp. Biol.* **63**, 53–83.

BENNET-CLARK, H. C. (1977). Scale effects in jumping animals. In *Scale Effects in Animal Locomotion*, (ed. T. J. Pedley). London: Academic Press.

BENNET-CLARK, H. C. & ALDER, G. M. (1979). The effect of air resistance on the jumping performance of insects. *J. exp. Biol.* **82**, 105–121.

BENNET-CLARK, H. C. & LUCEY, E. C. A. (1967). The jump of the flea: a study of the energetics and a model of the mechanism. *J. exp. Biol.* **47**, 59–76.

BROWN, R. H. J. (1963). Jumping arthropods. *Times Science Review*, summer 1963, pp. 6–7.

BROWN, R. H. J. (1967). Mechanism of locust jumping. *Nature, Lond.* **214**, 939.

CURREY, J. D. (1967). The failure of exoskeletons and endoskeletons. *J. Morph.* **123**, 1–16.

DUARTE, A. J. (1938). Problems of growth of the African migratory locust. *Bull. ent. Res.* **29**, 425–456.

ELLIS, P. E. (1951). The marching behaviour of hoppers of the African migratory locust, *Locusta migratoria migratorioides* (R. & F.), in the laboratory. *Anti-Locust Bulletin*, No. 7. London: Anti-Locust Research Centre.

EVANS, M. E. G. (1972). The jump of the click beetle (Coleoptera, Elateridae) – a preliminary study. *J. Zool., Lond.* **167**, 319–336.

EVANS, M. E. G. (1973). The jump of the click beetle (Coleoptera: Elateridae) – energetics and mechanics. *J. Zool., Lond.* **169**, 181–194.

GABRIEL, J. M. (1984). The effect of animal design on jumping performance. *J. Zool., Lond.* **204**, 533–539.

HALL-CRAGGS, E. C. B. (1965). An analysis of the jump of the lesser galago (*Galago senegalensis*). *J. Zool., Lond.* **147**, 20–29.

HEITLER, W. J. (1974). The locust jump: specializations of the metathoracic femoral-tibial joint. *J. comp. Physiol.* **89**, 93–104.

HEITLER, W. J. (1977). The locust jump. III. Structural specializations of the metathoracic tibiae. *J. exp. Biol.* **67**, 29–36.

HEITLER, W. J. & BURROWS, M. (1977*a*). The locust jump. I. The motor programme. *J. exp. Biol.* **66**, 203–219.

HEITLER, W. J. & BURROW, M. (1977*b*). The locust jump. II. Neural circuits of the motor programme. *J. exp. Biol.* **66**, 221–241.

HUNTER-JONES, P. (1961). *Rearing and Breeding Locusts in the Laboratory*. London: Anti-Locust Research Centre.

MAYNARD SMITH, J. (1968). *Mathematical Ideas in Biology*. Cambridge: Cambridge University Press.

PEARSON, K. G. & GOODMAN, C. S. (1981). Presynaptic inhibition of transmission from identified interneurons in locust central nervous systems. *J. Neurophysiol.* **43**, 501–515.

PEARSON, K. G., HEITLER, W. J. & STEEVES, J. D. (1980). Triggering of the locust jump by multimodal inhibitory interneurones. *J. Neurophysiol.* **43**, 257–277.

PENNYCUICK, C. J. & PARKER, G. A. (1966). Structural limitations on the power output of the pigeon's flight muscles. *J. exp. Biol.* **45**, 489–498.

PFLÜGER, H.-J. & BURROWS, M. (1978). Locusts use the same basic motor pattern in swimming as in jumping and kicking. *J. exp. Biol.* **75**, 81–93.

STEEVES, J. D. & PEARSON, K. G. (1982). Proprioceptive gating of inhibitory pathways to hindleg flexor motoneurons in the locust. *J. comp. Physiol.* **146**, 507–515.

WEIS-FOGH, T. & ALEXANDER, R. MCN. (1977). The sustained power obtainable from striated muscle. In *Scale Effects in Animal Locomotion*, (ed. T. J. Pedley). London: Academic Press.