

THE DEVELOPMENT OF THE LOCUST JUMPING MECHANISM

II. ENERGY STORAGE AND MUSCLE MECHANICS

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SUMMARY

1. In an escape jump, the adult locust extensor tibiae muscle produces more than twice the specific energy output of the fourth instar muscle.

2. If forced to jump repeatedly, the extensor muscles of hoppers and adults produce the same specific energy output.

3. In escape jumping, specific energy production increases with age within an instar, but this does not seem to be the case in repeated jumping over a 10-min period.

4. Adult locusts have thicker cuticle, including thicker semilunar processes, than hoppers. They also have relatively larger extensor apodemes. The cuticle thickness of all instars increases with age up to apolysis or maturity.

5. The fourth instar extensor muscle has a lower angle of pennation and relatively longer muscle fibres than the adult muscle.

6. The stiffness of the semilunar processes increases with age both within and between instars, so that the mature adult leg has the highest energy storage capacity.

7. To produce the required amount of energy storage, the adult muscle fibres must shorten slightly more than those of the fourth instar, but they must produce more than twice the force per unit area.

8. The strain on the apodeme is similar in adults and hoppers, and greater at the distal than at the proximal end.

INTRODUCTION

In the preceding paper (Gabriel, 1985), age-related changes in jumping performance were correlated with allometric growth and size. Here, the energy requirements for jumps by locusts of different ages and the necessary changes in the properties of the extensor muscle and energy storage system are examined.

Many jumping animals use energy storage systems. For an ectotherm, one advantage of storing energy is that high force may be produced even at low environmental temperatures (Bennet-Clark, 1975). Also, a great increase in take-

off velocity may be achieved with little additional weight; the stores of an adult female locust weigh under 4 mg per leg and are capable of storing the energy produced by 70 mg of muscle (Bennet-Clark 1975). Hard cuticle is used as an energy store by several jumping insects, e.g. the tanned scroll of the flea beetle (Ker, 1977) and the semilunar processes and extensor apodeme of the locust (Bennet-Clark, 1975).

Jensen & Weis-Fogh (1962) showed changes in the mechanical properties of the metathoracic tibia of the adult locust which were associated with the deposition of post-ecdysial cuticle. Scott & Hepburn (1976) have shown a positive correlation between femoral cuticular stiffness and maximum jumping force in grasshoppers and locusts. This correlation is also shown by locusts of different instars. The constraint of ecdysis, however, poses an additional engineering problem for the nymphal instars, as only limited post-ecdysial deposition is possible if the exoskeleton is to be successfully ruptured at the next moult. If present, allometric changes in cuticle thickness would affect the energy storage system. The scaling of cuticle thickness to limb segment length is also important when considering resistance to static and dynamic forces.

As the metathoracic femur grows allometrically, it can accommodate a greater proportion of extensor tibiae muscle. Allometry may also lead to differences in the form of the muscle, e.g. a greater angle of pennation of muscle fibres resulting in an increase in the effective mechanical advantage of a muscle (Alexander, 1983). The mechanics of the muscle are important when one considers the energy storage system. The muscle stress must be such as to strain the skeleton sufficiently to store the required energy.

This paper relates the mechanics of the extensor tibiae muscle to the energy storage capacity of the jumping leg of the locust. The load-deformation relationships for the semilunar processes of locusts of different ages are measured and related to the form of the legs. Changes in jumping performance within an instar are correlated with the changing properties of the energy storage system.

MATERIALS AND METHODS

Male desert locusts (*Schistocerca gregaria* Forskål) of the fourth and fifth instars and adult stages were used in these experiments. A minimum of five animals was used in each case. In addition to jump range and power output, energy production was calculated from the variables measured in the preceding paper (Gabriel, 1985). The energy, E , required for a jump can be found from:

$$E = mgd / 2\sin 2\theta,$$

where m = mass, g = acceleration due to gravity (9.81 m s^{-2}), d = jump range, θ = take-off angle (45° for maximum range). Specific energy (energy per kilogram of extensor muscle) was also calculated.

The methods for measuring and comparing dimensions were as described in the preceding paper, using the reference dimensions of $\text{mass}^{1/3}$ and, where

appropriate, metathoracic femur length. The standard reference dimension of mass^{1/3} cannot be used in the comparison of cuticle thickness within an instar, because mass itself changes.

The metathoracic legs were sectioned and cuticle thickness was measured at four sites, shown in semi-diagrammatic cross-sections of the adult leg in Fig. 1. In both instars, cuticle thickness was measured at the positions indicated. The thickness and width of the metathoracic extensor apodeme were measured at 10 equally-spaced positions. Apodeme length was also measured.

For the comparison of metathoracic extensor muscle structure, the left metathoracic femur length of each animal was measured. The leg was fixed in a flexed position, and the extensor muscle was exposed. Muscles were kept moist with locust Ringer (Usherwood & Grundfest, 1965) while measurements were taken. Fibre length and angle were measured on both sides of the apodeme, at several sites.

To measure the load-deformation properties of the semilunar processes, a method similar to that of Bennet-Clark (1975) was used. Deformation of the distal end of the semilunar process (the articulation of the joint) was measured with a Watson Bactil microscope fitted with a curtain micrometer eyepiece. The test legs were fixed horizontally onto balsa wood. Thread was fastened around the proximal head of the tibia and attached to a force transducer, mounted on a micromanipulator. Force was applied in parallel to the extensor apodeme by moving the transducer. The tibia was fixed firmly at its distal end and the force was applied close to the articulation, so the force on the articulation can be taken as virtually the same as the force applied.

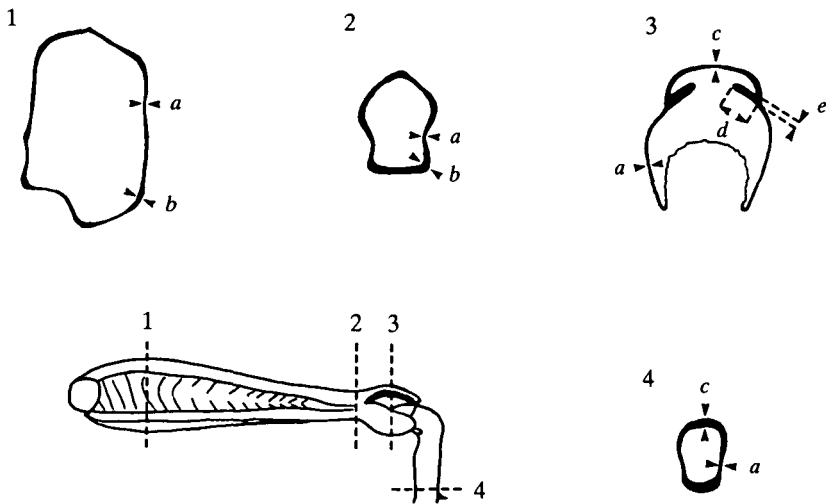


Fig. 1. Cross-sections of an adult locust femur and tibia at the four positions marked on the leg, showing the positions where cuticle thickness was measured in the fourth instars and adults.

RESULTS

Escape jump energetics

Fig. 2 shows the variation in specific energy requirements within and between different instars in producing an escape jump. On the day of hatching or moulting, specific energy production is low, but highly variable. The measured means fall between 7 and 17 J kg⁻¹, and no significant differences were found. The mature adult produces almost 70 J kg⁻¹ of extensor muscle, compared with a peak production of 45 J kg⁻¹ for the fifth instar, and less than 30 J kg⁻¹ for the younger hoppers; these values are significantly different.

When forced to jump repeatedly over a 10-min period the adult locust produces about the same specific energy (in J kg⁻¹) as the fourth and fifth instars (Table 1), even though the adult produces fewer, longer jumps (Gabriel, 1985).

The age within an instar has a marked effect on escape jump performance. However, if an animal is forced to jump over a long period of time, it produces the same specific energy or specific power output regardless of instar or age within the instar.

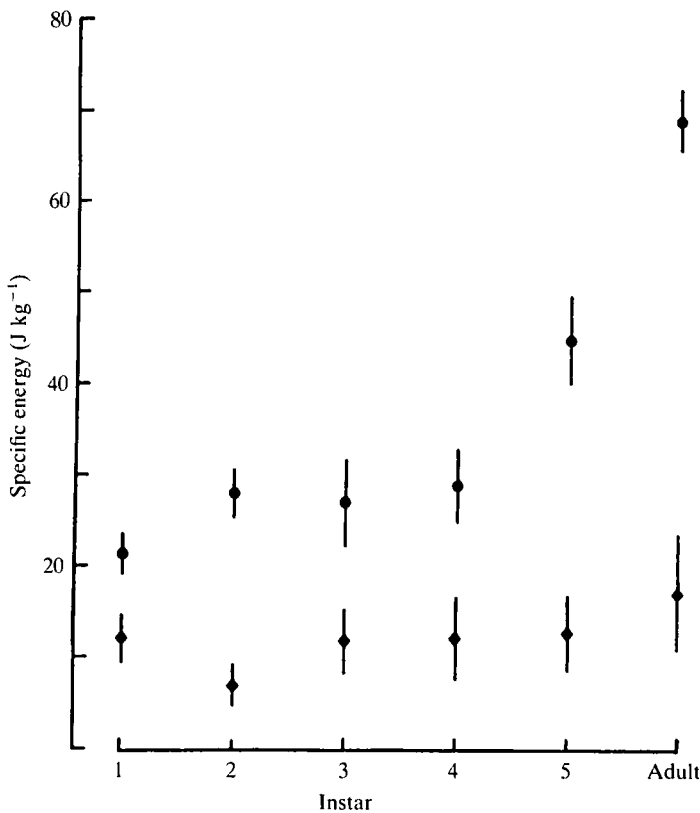


Fig. 2. Means and standard deviations of specific energy output of the extensor muscles required for each instar in an escape jump. Day 0 (◆); day of peak performance (●). $N=5$.

Table 1. *Specific energy ($J kg^{-1}$) required in jumping for a 10-min period*

Instar	Age (days)						
	0	2	4	6	7	14	≥ 21
4	2306 (1048)	3469 (482)	3547 (716)	3256 (594)			
5				3538 (479)			
Adult	2387 (705)				3661 (658)	3354 (518)	3335 (1060)

Mean for five animals. Standard deviation given in brackets.

Cuticle thickness

If isometry were maintained, division of cuticle thickness measurements by $mass^{1/3}$ would give equal values for any particular phase of each instar. For all variables measured, however, the values obtained for the adults are much higher than those for the hoppers, with the F-ratios highly significant (Table 2). Fig. 3 shows this increase in relative cuticle thickness for semilunar process ridge length (dimension 3*d*) and width (dimension 3*e*).

Variation in thickness of these dimensions occurs within the adult stage (Table 3). There is a significant increase in cuticle thickness in older animals. Most of the increase in thickness occurs within 7 days of ecdysis.

Apodeme dimensions

In both the fourth instar and the adult, the extensor apodeme occupies the same fraction of the length of the femur [0.80 of the length of the fourth instar femur and 0.82 of the adult femur; no significant difference (Student's *t*-test)]. Obviously, as the adult femur is proportionately longer than that of the fourth instar, the adult apodeme is also proportionately longer.

Table 2. *Mean values of cuticle thickness divided by $mass^{1/3}$*

Dimensions measured	Instar						Adult	F-ratio
	1	2	3	4	5			
1 <i>a</i>	0.016	0.012	0.019	0.014	0.012	0.037	23.31	
1 <i>b</i>	0.027	0.022	0.037	0.036	0.042	0.075	33.32	
2 <i>a</i>	0.019	0.015	0.021	0.031	0.016	0.048	24.80	
2 <i>b</i>	0.037	0.035	0.042	0.049	0.046	0.090	22.12	
3 <i>a</i>	0.015	0.017	0.019	0.014	0.010	0.035	14.76	
3 <i>c</i>	0.018	0.016	0.020	0.011	0.014	0.028	8.05	
3 <i>d</i>	0.261	0.205	0.223	0.236	0.278	0.486	71.57	
3 <i>e</i>	0.092	0.085	0.097	0.092	0.114	0.156	13.80	
4 <i>a</i>	0.022	0.014	0.022	0.014	0.017	0.042	18.44	
4 <i>c</i>	0.033	0.030	0.037	0.022	0.032	0.081	9.97	

Dimensions listed are those shown in Fig. 1. Values in $mm g^{-1/3}$.

All F-ratios are highly significant, with 5,24 degrees of freedom.

N = five locusts, in each case.

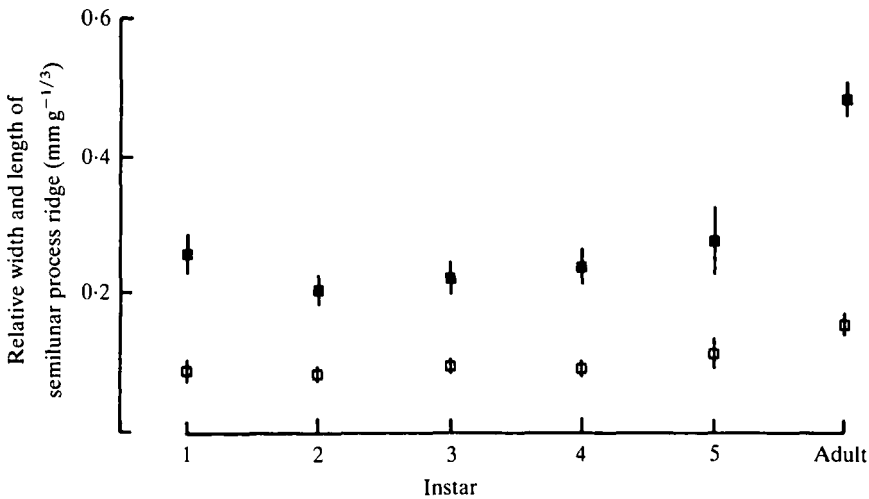


Fig. 3. Means and standard deviations for cuticle thickness divided by mass^{1/3}. Semilunar process ridge length (■); semilunar process ridge width (□). *N* = 5.

Fig. 4 shows the variations in thickness and width that occur along the length of the extensor apodemes. The fourth instar apodeme increases in width from a relatively more distal position (i.e. closer to the joint), though the muscle insertions begin at a similar point in both cases – 30% of the length away from the distal expansion. In geometrically similar animals, areas should be proportional to mass^{2/3}. The area of extensor muscle insertion can be estimated from the area under the 'width' curves. The areas obtained (for two legs) are 35.6 mm² for the adult and 9.04 mm² for the fourth instar, giving 25.9 mm² g^{-2/3} for the adult and 15.8 mm² g^{-2/3} for the fourth instar. Thus the adult has a relatively larger area for extensor muscle insertion. This would be expected from the relatively larger mass of the adult muscle (Gabriel, 1985).

For each position along the apodeme length, the cross-sectional areas have been

Table 3. *The mean and standard deviation values for dimensions 3d and 3e divided by femur length, in adults in different ages*

		Mean	s.d.	Significance
3d	1 day	0.0168	0.0031	Mann-Whitney rank tests confirmed a trend of increasing thickness with age. <i>P</i> < 0.01
	7 days	0.0186	0.0030	
	14 days	0.0227	0.0040	
	Mature	0.0270	0.0004	
3e	1 day	0.0054	0.0015	One-way ANOVA gave F-ratio = 7.522, 3, 16 df, <i>P</i> < 0.005
	7 days	0.0074	0.0007	
	14 days	0.0074	0.0011	
	Mature	0.0087	0.0009	

For dimension 3e, the means of the 1-day-old and 7-day-old animals were shown to be significantly different at *t* = 2.869, 16 df, *P* < 0.025. There were no other significant differences.

N = five locusts in each case.

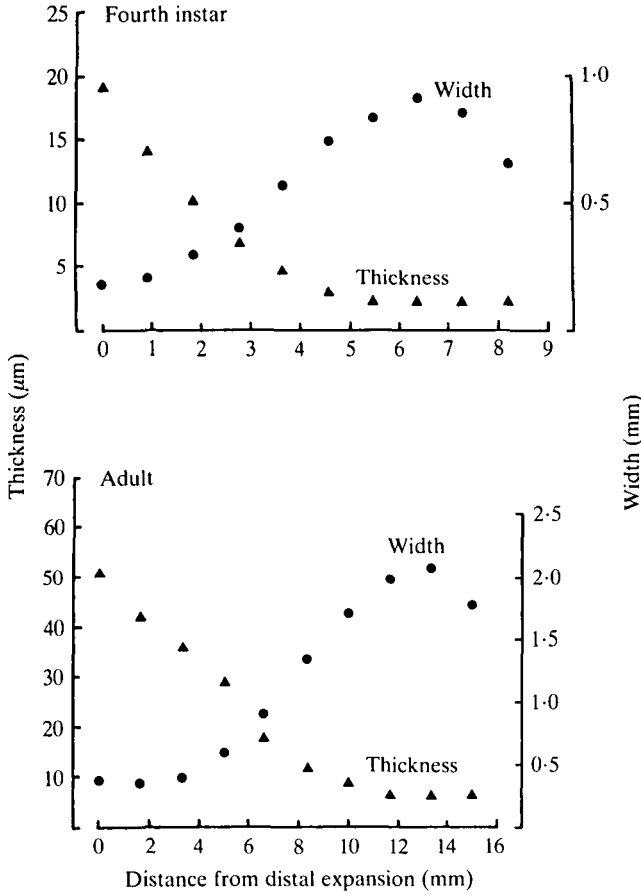


Fig. 4. Apodeme thickness (▲) and width (●) at 10 positions along the length in fourth instars and adults. *N* = 5.

calculated, and compared by regression analysis using the equally spaced position numbers as *x* values. The slopes are not significantly different, but the *y*-intercept is higher for the adult (Fig. 5), indicating that a relatively greater force may be taken by the adult apodeme. The values obtained are as follows:

$$\begin{aligned} \text{fourth instar: } \text{area} &= -0.034x + 0.59, \\ \text{adult: } \text{area} &= -0.050x + 1.40. \end{aligned}$$

In both cases, cross-sectional area decreases proximally; this is to be expected as only the distal portion of the apodeme is required to take the full force of muscular contraction, and force will decrease proximally.

Muscle fibre angles and lengths

Fig. 6 shows the change in angle of pennation and relative fibre length (i.e. fibre length as a proportion of femur length) between the fourth instar and adult stages. The muscle patterns are drawn to different scales, so that apparent femur length is the same. Two-way analysis of variance indicates that the greatest variation

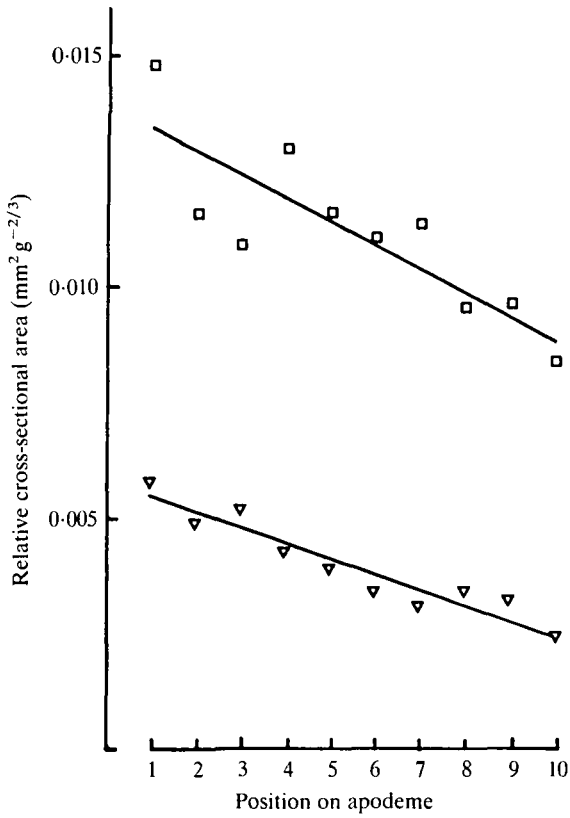


Fig. 5. Apodeme cross-sectional area at 10 positions along the length in fourth instars (∇) and adults (\square). Least squares regression lines are also shown.

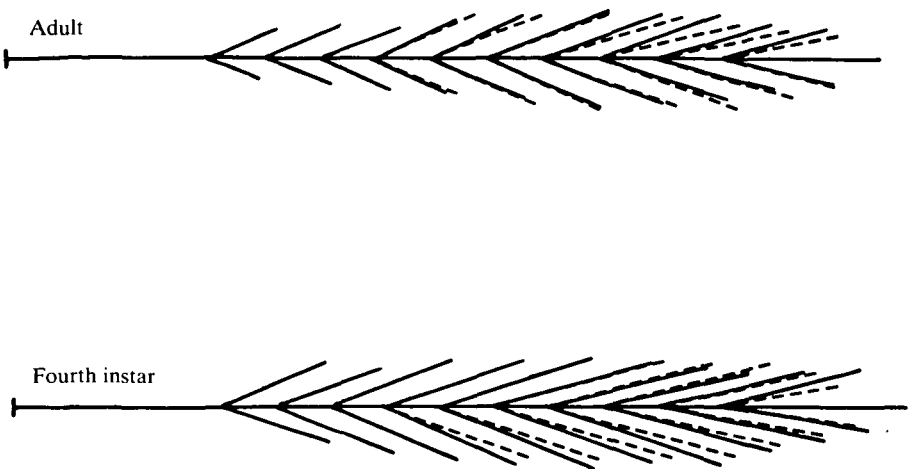


Fig. 6. The relative fibre lengths and the angles of pennation of the extensor muscle of fourth instar and adult locusts ($N=5$ in each case). Total length of fourth instar apodeme, 8.6 mm. Total length of adult apodeme, 17.6 mm. Solid lines represent the ventral fibres. Dotted lines represent fibres within the body of the muscle.

occurs between instars ($F > 170$ for angle and $F > 350$ for length), although significant variation also occurs along the length of each leg ($F > 25$ for angle and $F > 13$ for length). The mean angle of pennation was 16.2° for the fourth instar and 19.8° for the adult. These values were significantly different at the $P < 0.01$ level ($t = 3.167$, 296 df). The mean value of fibre length divided by femur length was 0.175 for the fourth instar and 0.132 for the adult. These values were significantly different at the $P < 0.001$ level ($t = 4.594$, 296 df). The extensor muscle of the fourth instar has a lower angle of pennation and relatively longer muscle fibres than that of the adult. The actual mean fibre length for the fourth instar was 1.96 ± 0.26 mm. For the adult, it was 2.90 ± 0.57 mm.

Load-deformation experiments on the semilunar processes

In the analysis of these results, load is taken as the independent variable and deformation as the dependent variable. Scatterplots of load against deformation for both methods showed the data to have a heteroscedastic distribution. Logarithmic transformation was necessary to correct for this. Fig. 7 shows the

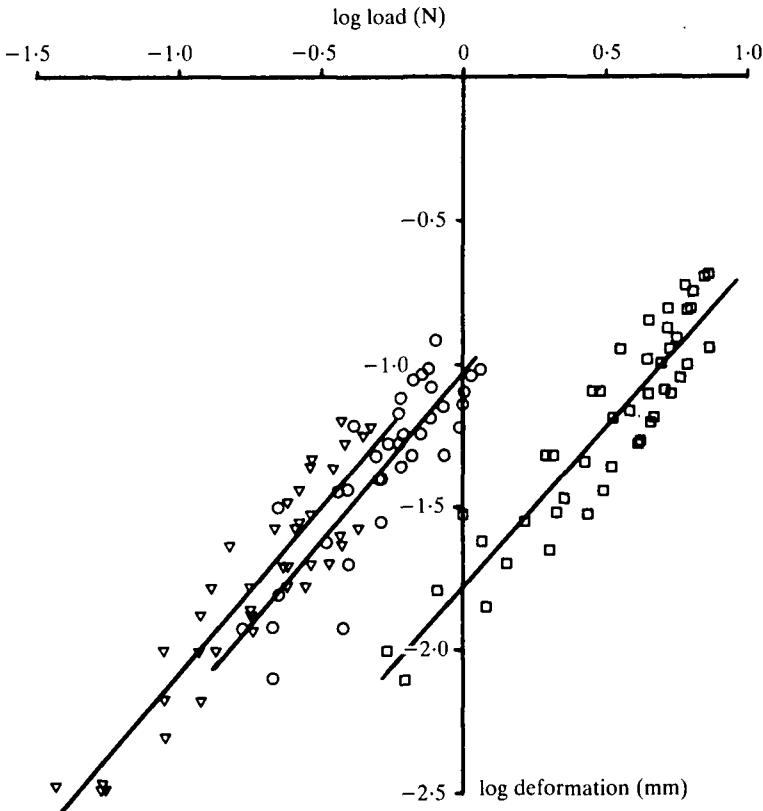


Fig. 7. Fitted regression lines for log deformation against log load in fourth instar (∇), fifth instar (\circ) and adult (\square) locusts.

regression lines for males of the fourth, fifth and adult instars. The lines run parallel, with significant differences in the y-intercepts only, indicating differences in stiffness of the semilunar processes between instars as the adult semilunar processes deform less than those of the hoppers for a given load. The regression equations are given in Table 4.

Table 5 shows regression equations for adult animals of different ages (1, 7 and 14 days after ecdysis, and mature animals). There is a trend towards a more negative y-intercept with increased age. This means that for a given load, the semilunar processes of older animals will deform less than those of younger animals, i.e. the semilunar processes of older animals are stiffer.

Muscle contraction and energy storage

'Muscle contraction' can mean muscle shortening or force generation or both. In this case, both are important; the degree of shortening determines the possible deformation of energy stores, but if there is insufficient force, the stores cannot be deformed. I calculate here the force required for sufficient energy storage to produce an escape jump in fourth instar and adult locusts. The muscle strain necessary to produce the required deformation of the energy storage system elements is also calculated.

Young's modulus of the extensor apodeme is assumed to be equal in fourth instar and adult locusts. Young's modulus (Y) for adult locust extensor tibiae apodeme has a value of 19 kN mm^{-2} (Bennet-Clark, 1975). To simplify calculations, the lateral walls of the femur are assumed to be rigid, i.e. they do not deform when the extensor muscle contracts. An additional assumption for some calcula-

Table 4. *Fitted regression equations for loading of the semilunar processes in different instars*

Instar		95 % confidence limit on y-intercept
Fourth	$\log \text{ def} = 1.17 \log \text{ load} - 0.92$	± 0.17
Fifth	$\log \text{ def} = 1.18 \log \text{ load} - 1.03$	± 0.30
Adult	$\log \text{ def} = 1.11 \log \text{ load} - 1.78$	± 0.36

Deformation (def) in millimetres, load in newtons.

Table 5. *Fitted regression equations for loading of the semilunar processes of adult locusts, at different times after ecdysis*

Time after ecdysis		95 % confidence limit on y-intercept
1 day	$\log \text{ def} = 1.33 \log \text{ load} - 0.82$	± 0.16
7 days	$\log \text{ def} = 0.86 \log \text{ load} - 1.34$	± 0.32
14 days	$\log \text{ def} = 0.78 \log \text{ load} - 1.44$	± 0.35
Mature	$\log \text{ def} = 0.91 \log \text{ load} - 1.65$	± 0.30

Deformation (def) in millimetres, load in newtons.

tions is that the average values of angle of pennation and fibre length can be taken to represent the whole muscle, i.e. the force required per unit area for each of the muscles is calculated using the mean angle of pennation. The consequences of these assumptions will be discussed later.

The animals have the characteristics given in Table 6. The fourth instar male locust needs to produce 0.33 mJ per leg to jump 0.26 m. The adult male locust needs to produce 3.77 mJ per leg to jump 0.88 m. The energy storage system will be treated as three units working in series (c.f. Bennet-Clark, 1975), i.e. the semilunar processes, the distal apodeme (the region with no muscle attachment) and the proximal apodeme (where the extensor muscle attaches).

(1) Energy stored in the semilunar processes for any particular force can be calculated by integration using the regression equations for loading of the semilunar processes (Table 4) used in the form:

$$\begin{aligned} \text{fourth instar: deformation} &= 0.120 \text{ load}^{1.17}, \\ \text{adult: deformation} &= 0.017 \text{ load}^{1.11}. \end{aligned}$$

(2) Energy stored in the apodeme is found by calculating the deformation of the apodeme for a particular load from the Young's modulus. As force will vary along the proximal portion of the apodeme (with the distribution of muscle insertions), an average force of half of that chosen for the distal apodeme was used. The calculations for energy storage in the apodeme do not take into account either changes in cross-sectional area along the apodeme length or changes in cross-sectional area of the apodeme as it is loaded.

The values of force in the distal apodeme giving the required energy storage are given in Table 7. The values giving the nearest approximation to the required energy totals are 1.8 N for the fourth instar system, and 12.7 N for the adult

Table 6. *The characteristics of the animals used in the calculations in energy storage*

	Fourth instar	Adult	Notes
Mass (g)	0.519	1.738	
Percent jumping muscle	4.3	6.3	
Range (m)	0.260	0.884	
Energy per jump (mJ)	0.662	7.536	
Muscle per leg (g)	0.011	0.055	
Fibre length (mm)	1.96	2.90	
Pennation angle (°)	16.2	19.8	
Cross-sectional area of muscle per leg (mm ²)	5.7	18.9	calculated from fibre length assuming density of 1 mg mm ⁻³
Cross-sectional area of distal apodeme (mm ²)	0.0032	0.0173	
Apodeme length (mm)	2.6	5.0	measured from tibial insertion to muscle
Cross-sectional area of proximal apodeme (mm ²)	0.0023	0.0159	
Apodeme length (mm)	6.0	12.6	measured from distal to proximal muscle insertions

Table 7. *Energy storage per leg in the semilunar processes, distal and proximal extensor apodeme*

	Fourth instar	Adult
Semilunar processes		
Δl (mm)	0.241	0.286
E (mJ)	0.198	1.723
Distal apodeme		
$\Delta l/l$	0.030	0.039
Δl (mm)	0.077	0.193
E (mJ)	0.069	1.228
Proximal apodeme		
$\Delta l/l$	0.021	0.021
Δl (mm)	0.124	0.265
E (mJ)	0.056	0.842
Total mechanical energy stored (mJ)	0.323	3.793
Deformation of semilunar processes and distal apodeme (mm)	0.318	0.479
Deformation of semilunar processes and all apodeme (mm)	0.442	0.734

A force of 1.8 N is applied in the case of the fourth instar, and 12.7 N in the adult.
 $\Delta l/l$ = strain, Δl = deformation and E = energy.

system (Gabriel, 1983). With these figures, the muscle strain necessary to produce the required amount of deformation of the energy stores can be calculated.

For the fourth instar animal, the distal fibres must shorten by approximately 21 %, and the proximal fibres by 22 %, to produce the required deformation of the energy stores. For the adult animal, the fibres must shorten by a greater amount, 24–25 %. The force per unit cross-sectional area of the muscle fibres required for the fourth instar is 0.33 N mm^{-2} , whereas for the adult it is more than twice this, at 0.71 N mm^{-2} .

Deformation of the lateral walls has been ignored in these calculations. However, the error caused by this omission is likely to be small in both cases – large deformations of the lateral walls in response to muscle contraction would prevent the storage of energy in other leg components.

From Table 7 it can be seen that the adult should store a higher proportion of its total stored energy in the apodeme. The calculated strains in the apodeme are, however, quite similar. The distal apodeme of the fourth instar should strain by 3.0 %, compared to 3.9 % for the adult. For the proximal apodeme, 2.1 % strain is required for both stages. This suggests that the initial assumption of similar mechanical properties for fourth instar and adult apodemes was reasonable.

DISCUSSION

In the preceding paper (Gabriel, 1985), adult locusts were shown to have a greater jump range than hoppers, due partly to an increase in absolute size (applies to power-limited jumpers only) and partly to allometric growth. It has been shown in this paper, that there is a concomitant increase in the specific

energy requirement, with the adult needing substantially more specific energy than the young hoppers.

Hoppers, like adults, must store energy in a system of cuticular springs to amplify the specific power available from muscle contraction because they produce more specific power during take-off than is theoretically possible by direct muscle action alone. An additional indication that locusts of all ages store energy prior to escape jumps is their ability to jump well 'straight from the fridge'. Locusts can produce escape jumps of their usual length immediately upon removal from a coldroom, at 4°C (unpublished observation), when the power output of the muscles must be very low. As would be expected, the energy storage time appears to be longer. These properties would be expected from any energy storage system where contraction of a muscle is used to deform another material *to a particular value of strain*.

In producing a longer jump, the adult produces approximately the same specific power output during take-off as the hoppers (Gabriel, 1985). As the actual specific power produced by the muscle should be constant between instars, they probably use a similar amount of power amplification (power amplification is the ratio of power produced during take-off to power produced in muscle contraction and simply reduces to the ratio of energy storage to release time). Even with a similar amplification factor, differing energy output could be found, as shown experimentally (Fig. 2), if the adults are capable of generating more force and use stiffer cuticular springs. The production, by the fourth instars and adults, of the same total specific jump energy in a 10-min period of repeated jumping but not in a single escape jump, can also be accounted for by the use of stiffer cuticular springs, without changes in the power production of the muscle. The data on specific energy production within instars support this idea.

The relatively larger extensor muscle of the adult, with its higher pennation angle, increased cross-sectional area and increased area of insertion on the apodeme and femoral cuticle allows the production of relatively higher forces. The lengthening and thickening of the semilunar processes and the relative increase in cross-sectional area of the extensor apodeme result in a stiffer spring system in the adult leg. The use of a stronger muscle and stiffer springs thus allows an increase in energy storage capacity for a given strain. Strain in the cuticular springs would be a useful measure of the mechanical safety of the system, as well as of energy stored. If the system were set to trigger at a particular value of strain, of for example the semilunar processes, the adult would be able to store relatively more energy (per unit of extensor muscle mass) than the fourth instar. The animal would not need any change in its neurophysiological control to effect this increase in energy storage. The presence of a similar joint design (Gabriel, 1985), with stiffer springs in the adult, supports this hypothesis because it allows a similar trigger mechanism for the catapult system.

In both instars, a large strain is required to store sufficient energy for an escape jump. The fourth instar, however, needs to produce less than half the force per unit area of muscle fibres required by the adult. It is likely that the adult is producing close to its maximum force, but this does not seem to be the case for the fourth instar muscles (Gabriel & Sainsbury, 1982).

There are concomitant increases in cuticle thickness and stiffness of the semilunar processes both within and between instars. An increase in stiffness of the energy storage system within an instar would be expected to have a similar effect to increasing stiffness between instars, i.e. an animal with stiffer springs could store more energy for the same degree of deformation, assuming the muscle can produce sufficient force to deform the energy store.

The dorsal-to-ventral height of the tibia increases disproportionately in the adult stage (Gabriel, 1985) and it was suggested that a disproportionate increase in tibial cuticle thickness would be necessary to counteract the increased likelihood of local buckling: this increase in cuticle thickness has been shown to occur. The metathoracic leg of the hoppers will sometimes fail by local buckling in the narrow distal portion of the femur, when the extensor muscle is stimulated electrically (unpublished observation). Under normal conditions, the animal is unlikely to strain its own cuticle to failure. The cuticle of the legs of the hoppers is strengthened by the presence of longitudinal folds, which also allow the expansion of the leg during an instar to accommodate the increase in muscle mass. The adult has less obvious folds, but disproportionate increases in the thickness of the cuticle in the femur are necessary to compensate for relatively higher forces in the jumping system at the adult stage. The necessity of changes in cuticle thickness for increased jumping performance is accentuated by comparison with the design of other arthropod limbs; for example, spiders and cockroaches have been shown to exhibit isometry in cuticle thickness (Prange, 1977).

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