ONTOGENETIC SCALING OF JUMP PERFORMANCE IN THE AFRICAN DESERT LOCUST (*SCHISTOCERCA GREGARIA*)

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Summary

Ontogenetic growth was used as a model for the effect of body size on jumping performance of the African desert locust (*Schistocerca gregaria*). Using models that generated relationships between morphology and body size proposed by McMahon and the relationships between morphology and performance described by Hill, we generated testable predictions of how jumping performance measures may change as a function of body mass. Data were collected over an ontogenetic sequence that ranged from 1-day-old first instars to 45-day-old adults. Performance was quantified using a high-sensitivity, three-dimensional force plate. Performance parameters quantified included the force, acceleration, take-off velocity, kinetic energy and power output. With the exception of power output, each measure of performance scaled to body mass in a manner consistent with the predictions of the elastic similarity model. Power output scaled to body mass in a manner consistent with the predictions of the constant stress similarity model. As we noted previously for the scaling of flexural stiffness of the metathoracic tibiae, the elastic similarity model is approximated by the performance of the locust in spite of the morphological design that deviates from that model's predictions.

These results indicate that the jump has separate functions in the flightless juvenile instars and in the flying adult stage of the life history. Juvenile locusts produce take-off velocities of between 0.9 and $1.2 \, \mathrm{m \, s^{-1}}$ that are relatively scale-independent. The take-off velocity in juveniles produces a distance of ballistic travel that averages between 20 and 30cm. In adults, the take-off velocity is also relatively scale-independent at a level approximately twice as high as in juveniles (i.e. $2.5 \, \mathrm{m \, s^{-1}}$). This velocity is coincident with the minimum flight speed reported by Weis-Fogh and a minimum flight speed that we have estimated using actuator disc theory. We suggest that, in juveniles, the jump is designed to achieve a characteristic distance travelled and in adults the jump is designed to achieve a minimum velocity necessary to fly.

Introduction

The design of animal locomotion mechanisms balances structural, material and power-generating propulsive system designs to achieve effective levels of locomotor performance. Further, these design issues must be balanced within the constraints

imposed by biological manufacturing processes. Because animals come in a great range of body sizes, balancing these design features must accommodate changes in mechanics that result from changes in scale. There is already a wealth of scaling studies in zoology that have largely been performed to examine the effects of scale on skeletal designs *via* interspecific comparison between functionally similar, but morphologically distinct, species (see, for example, McMahon and Bonner, 1983). The ontogenetic scaling of skeletal design in *Schistocerca gregaria* provides a great opportunity to investigate in detail the scaling of design in functionally and morphologically similar animals. In the study of scaling of skeletal design it is believed that a connection can be made between the morphological design of anatomical features and their functioning (McMahon, 1973). In this paper, we examine the scaling of jumping performance in the African desert locust to see if there is a connection between functional and morphological design.

In a previous paper we described a scaling relationship for limb lengths in the African desert locust (*Schistocerca gregaria*) that produced relatively longer and slimmer limb segments in larger locusts (Katz and Gosline, 1992), an observation that was at variance with any existing scaling model (McMahon, 1973, 1984; Bertram and Biewener, 1990). We suggested that the observed scaling relationship between limb shape and body size might represent a design feature associated with a jumping mode of locomotion. In order to evaluate this hypothesis, we need to know how the mechanical loading of the limb segments is related to size across the same ontogenetic sequence.

Previous work of other investigators has provided some of this information, but the literature contains conflicting information about the relationship between force production and body size in jumping locusts. Bennet-Clark (1977) showed that the distance travelled as the result of a jump is directly proportional to the velocity produced in the jump impulse and that velocity is the result of an acceleration developed over a time interval. However, the accelerations produced in the jump are inversely proportional to the leg length of the jumping animal. The functional significance of this relationship is manifest in the relatively longer legs of jumping animals, to reduce loading in the leg skeleton, and the relatively higher accelerations in smaller animals because of their absolutely shorter legs. For typically observed accelerations he cites one and a half gravities (g) for larger vertebrates, such as leopards and antelope, all the way up to $200g$ for the 0.45mg rat flea (Bennet-Clark and Lucey, 1967), with mean accelerations of about $24\,g$ for first-instar *S. gregaria* and about $10\,g$ for adults (Bennet-Clark, 1977). For adult locusts peak accelerations of about $18\,g$ are reported (Bennet-Clark, 1975).

In contrast, Scott and Hepburn (1976) reported that across the ontogenetic sequence of *Locusta migratoria* there is a relatively constant peak acceleration of about $10\,g$ produced in the jump impulse. They also report that this relationship is demonstrated in a sample of six different species of locusts and grasshoppers, indicating that this relationship is consistent and general. Further, they observed a consistent relationship between adult, femoral cuticle stiffness and the forces in jumping. They concluded that constant acceleration produced in jumping was functionally significant in matching the changes that occur in cuticular stiffness over the same developmental increase in body mass. Thus, the mechanical properties of the locomotor structures are appropriately matched to the loads they encounter in normal use.

Gabriel (1985*a*) has reported that, over the first four instars, *Schistocerca gregaria* jump approximately the same distance, but the jump distance increases by about 300% in adults. Gabriel's data suggest that across the juvenile instars take-off velocity is similar. If the analysis of Bennet-Clark (1977) is correct, then as the accelerations fall in larger animals, the duration of force production must increase to produce the same take-off velocity (i.e. the integral of acceleration over time) across instars. However, if Scott and Hepburn (1976) are correct in suggesting that acceleration is a constant of $10g$ then the duration of the force development is also a constant, regardless of leg length. These two predictions would not seem to be compatible, and without a resolution it is difficult to attempt any functional analysis of the morphological design programme described in our previous paper (Katz and Gosline, 1992).

It is also important to evaluate the functional significance of the jump performance to the animal. Others have suggested that how fast an animal accelerates is potentially adaptive in that prey that produce high accelerations are difficult to follow and catch (Emerson, 1978). As a result, the performance parameter that is thought to be the most functionally significant and has received the closest scrutiny is the acceleration produced in the jump. Emerson (1978) has proposed alternative models that either regulate acceleration or vary acceleration with increasing body size to discriminate strategies for predator avoidance in frogs. We will make the case that peak acceleration is not the critical design issue in the jump of the locust.

In this paper, we have attempted to quantify the loading experienced by the legs of the locust during the jump impulse. Using miniature force plate techniques we have measured the force, acceleration, velocity, displacement, kinetic energy and power output during ontogenetic development as well as the trajectory angle in the jump impulse of locusts on each day of life from the first day after emergence from the egg until full sexual maturity (day 45). The wide range of body mass covered by the locust has allowed us to determine scaling relationships for performance and to compare these relationships with existing models. The data provide clear evidence that the jump plays different roles in the locomotor performance of the locust at different times in its life history. The flightless, juvenile instars are jumping to achieve a functional distance and the adult locusts are jumping to achieve a velocity critical to the initiation of flight.

Materials and methods

Animal husbandry

Animals were sampled daily from a breeding colony of African desert locust (*Schistocerca gregaria*) maintained at the Department of Zoology at the University of British Columbia. The animals were kept at a constant temperature of 27°C, humidity of 56% and photoperiod of 13h:11h (L:D), and fed a diet of head lettuce and bran. A sample of five individuals was collected each day beginning on the first day following emergence from the egg until approximately 2 weeks after achieving sexual maturity (approximately 45 days).

Five jumps from each individual were examined, to give a total 25 jumps for each day in development. Each individual was weighed to the nearest 0.1mg after its final jump.

Occasionally, the jump event produced uninterpretable force traces due to transient, large-amplitude noise. Video images made during several of these jumps indicated that this was the result of slippage between the tarsus of the locust and the surface of the platform. Any jumps that showed evidence of transient forces were eliminated from the data set. As a result, there are varying sample sizes for each day. No assumptions were made as to the locust's motivation for jumping. There was no apparent multi-modality to the data on any given day that would have suggested that the jumps were distinguishable as 'escape jumps' or 'locomotor jumps'. Therefore, all jumps on a given day were treated as similar.

Adult locusts were allowed to jump with their wings intact and unencumbered. Control experiments where the wings of adults were held closed with cellophane tape were not significantly different in terms of peak force production from those where the wings were free to open (t_s=0.067, d.f.=14, P<0.05).

In this paper the term impulse is used in the same sense as that in Bennet-Clark (1975) in that it does not refer to the exchange of momentum explicitly, but to the interval of the jump that can be characterized by ground reaction forces above 1g.

The force plate

Fig. 1 is a diagram of the force plate used in this study. Vertical, horizontal and lateral forces produced in the jump of the locust were measured simultaneously with a force plate similar in design to that described by Full and Tu (1990), but modified to achieve higher sensitivity and frequency response. For instars 1–4, a balsa wood platform measuring 1.5 cm×0.75cm×0.15 cm was bonded to the end of a series of hollow brass box-beams. For fifth instars and adults, a larger, circular balsa wood platform measuring 2.5 cm in radius and 0.25cm thick was bonded to the pre-existing platform to provide a larger surface from which the larger locusts could jump. The force-sensing elements were similar to those described by Full and Tu (1990) in that semiconductor strain gauges (type SR4 SBP3-20-35 or SBP3-05-35, BLH Electronics, Canton, MA) were bonded to the outer surfaces of double cantilevers produced by machining windows in the sides of the box-beams. The mass of the platform was reduced to improve the frequency response by having only one set of double cantilevers for each of the three principal components of force application. The resonant frequencies ranged from a high of 1.543kHz for the most distal cantilever pair, to a low of 527Hz for the most proximal pair. Force sensitivity was enhanced by machining the leaves of the double cantilever down from a thickness of 0.015″ to a thickness of 0.007″. This modification produced a sensitivity of 12.60VN^{-1} for the most proximal gauge and a sensitivity of 28.30VN^{-1} for the most distal gauge.

Mechanical crosstalk between these gauges was low, but to minimize crosstalk further between the vertical and lateral gauges a small piece of telescoping box-tubing was welded into the lumen of the beam between the two sensitive elements. Serial calibrations in various orientations in three dimensions indicated that crosstalk interactions where a proximal gauge influenced a distal gauge produced less than a 1% change in the distal gauge output. This was deemed insignificant. Of the three potential interactions in the

other direction, only the interaction of the most distal gauge with the most proximal proved to affect the proximal gauge's output by more than 3% and this was addressed in the analysis by a recursive loop in the analytical process that estimated the actual output of the proximal gauge. At no time did noise exceed 5% of the signal magnitude. Therefore, no signal filtering was employed.

The resistive elements in the strain gauges formed half of a bridge circuit whose d.c. output was amplified and collected at a rate of 5kHz on three channels of a digital storage oscilloscope (Data Precision, Data 6000A Universal Waveform Analyzer, Analogic Co., Peabody, MA, USA), and transferred to an IBM-PC type computer *via* serial communications for later analysis.
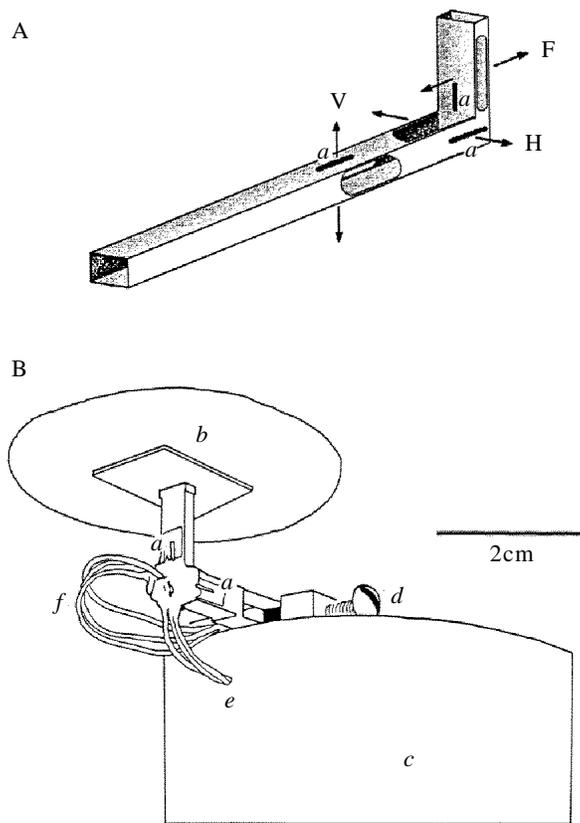

Fig. 1. (A) Diagrammatic sketch of the force plate used in this study viewed obliquely from above. This diagram shows the orientation of the double cantilever beams that sense forces in the vertical (V), horizontal (H) and fore–aft directions (F). *a* marks the position of the force-sensing strain gauges. (B) Diagram of the force plate used in this study viewed obliquely from below. *a* marks the position of the force-sensing strain gauges. *b*, balsa wood platform; *c*, base/reaction mass; *d*, machine screw attachment of platform to base; *e*, lead wires from the fore–aft gauge; *f*, lead wires from the horizontal gauge (the vertical gauge is obscured in this view).

Jumping arena

All jumps were performed under a clear acrylic dome enclosure. The dimensions of the enclosure were 0.45m wide by 0.33m deep by 0.58m tall. The force plate was placed in the centre of the floor of the enclosure on a sheet of sorbothane, vibration-dampening rubber. A balsa wood surface measuring 0.25m by 0.15m was constructed with a hole the same size and shape as the force platform. This surface was placed in the enclosure so that the force plate became a small portion of a larger, relatively continuous, surface from which the locusts could jump. For each jump event the locust was placed on the force-sensing portion of the wooden surface and allowed to jump freely. Reluctant individuals were enticed to jump with loud noises or abrupt movements in their visual fields. No electrical stimulation was employed. The possibility that this enclosure inhibited the performance of the locusts was not investigated.

Data analysis

The three digitized signals were resolved *via* vector addition into two arrays: one contained the resultant force vector and the other an angle to the horizontal for each 200 μs sample. A baseline of 0N was established by estimating the mean value of the first 83 data points (i.e. one period of a 60Hz noise signal) in each array preceding the jump with the animal on the force plate. As such, each force value in the vertical direction was referenced to newtons beyond one body weight. The beginning (or ending) of the jump impulse was defined by the force rising above (or falling below) a threshold level that was 2.5% of the maximum force. Force values were normalized by body mass to produce an array representing the instantaneous acceleration. Each acceleration array was integrated numerically to produce the velocity developed by the centre of gravity for each moment in the jump impulse. The initial value of velocity was assumed to be zero, and the velocities were integrated to calculate the displacement of the centre of gravity at each moment in the jump impulse. Additionally, the product of the ground reaction force and velocity arrays gave the power produced in the jump. The values of end-impulse velocity and body mass were used to calculate the kinetic energy (E_K) produced in the jump with the familiar formula:

$$E_K = \tfrac{1}{2}\text{mass}(\text{velocity})^2.$$

The horizontal distance covered by the jump was estimated using the ballistic equations reported by Bennet-Clark (1975).

Statistics

Except where noted, all statistical tests were chosen on the basis of criteria presented in Sokal and Rohlf (1981). All relationships were judged significant at the 0.05 probability level. Statistical tests were performed using the STATGRAPHICS (STSC, MA, USA, Ver. 5) statistical software package.

Results

Fig. 2 is a representative data set from a single jump of a 0.5007g fourth-instar locust.

The force envelope shows the relatively slow development of force and the rapid fall in force. The entire impulse lasted 32.8ms, and peak force was achieved at approximately 27ms, or approximately 82% of the impulse duration. In both first instars and adults the time of peak force shifted to later in the impulse duration. This resulted in a relatively more rapid fall in force following the peak force output. Thus, there are subtle differences in the shape of the acceleration envelope that have consequences for the estimation of performance that will be discussed below. This force production profile is not consistent with the optimum described by Bennet-Clark (1977) for minimizing the mass of the skeleton. He suggested that force should be produced at a constant level during a jump impulse so that large-magnitude forces do not produce intolerably high stresses in the skeleton. Ker (1977) has pointed out that a force envelope like that in Fig. 2 is the consequence of the coupling of an unloading, elastic energy storage device with rapidly decaying force to a mechanical lever system that is increasing its mechanical advantage to take advantage of that decaying force.

Within each impulse the angle that the force vector makes with the horizontal (i.e. the trajectory angle) did not seem to change significantly or systematically. The standard error of the trajectories within a single jump impulse had a high value of 1.6° in first
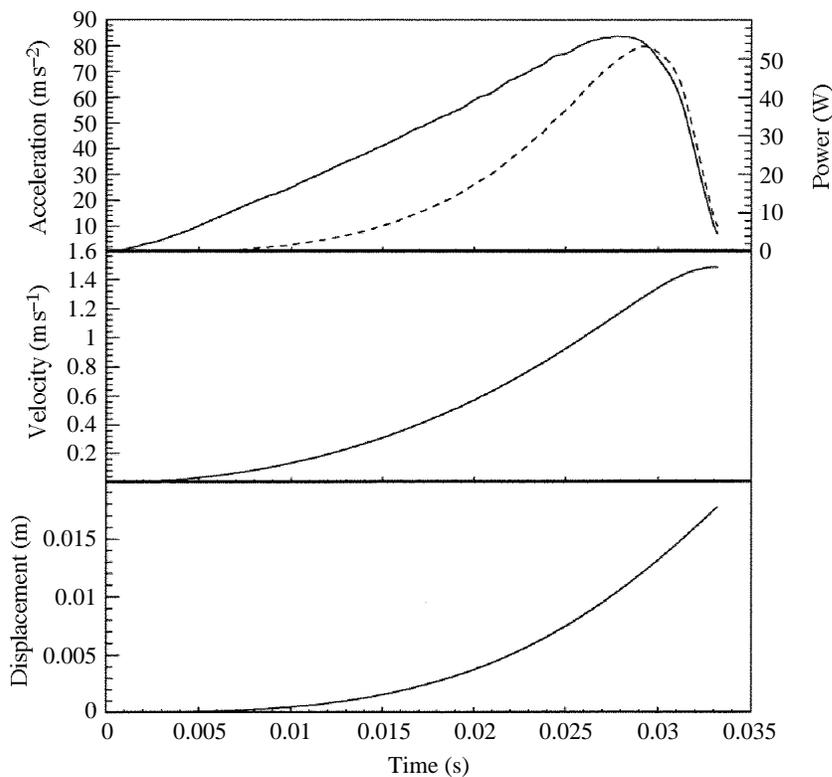

Fig. 2. Sample output for a 0.5007g fourth-instar individual showing the time course of acceleration (solid line), velocity, movement and power production (dashed line). Calculations of the various measures of performance are described in more detail in the text.

instars and a low value of 0.3° in adults. Inspection of the arrays of trajectory angles indicated that the data were not stationary, with the majority of the variation in the data occurring early in the jump impulse when the forces were low and the vector addition of the relatively noisy force arrays produced relatively high variability of the calculated angles. After the approximate one quarter point in the impulse, the forces are higher, making the signal to noise ratio larger, and the variance of the trajectory angles is even smaller than calculated for the entire time series. This means that it is a fair approximation to assume constant trajectory angle and to integrate the acceleration and velocity arrays as scalar rather than vector variables to calculate velocity and distance moved by the centre of gravity, respectively. It also suggests that there is a large degree of stability built into the design of the jumping mechanism of these locusts. The time course of the jump impulse (approximately 15ms in first instars) makes it unlikely that a neural reflex is capable of modulating muscular control over the jumping mechanism to make fine adjustments to trajectories during the impulse.

There is a sexual dimorphism in body mass that develops in the adults, where females become 50–75% heavier than males. Analysis of covariance indicated that for juvenile instars there was no significant effect of sex beyond the effect of body mass on any of the variables examined (ANCOVA, F_s=3.133, d.f.=1,447, for peak acceleration on body mass, the relationship most closely approaching significance.) As such, the data for both sexes were pooled for all juvenile instars for the purposes of performing regressions. In the case of the relationship between movement of the centre of gravity and body mass there was no significant effect of sex beyond the effect of body mass for the entire life history (ANCOVA, F_s=2.737, d.f.=1,874). Therefore, both sexes and all age classes were pooled only for this data set for the estimate of the scaling of this one parameter. The distinction between juvenile and adult locusts in the context of scaling is not completely arbitrary, as the jump itself may have different functional significance in different stages of the life history (see below).

Both the relationships of body mass and peak ground reaction force as functions of age describe sigmoid curves. Body mass increased in a logistic way before levelling off near the end of the fifth instar (Fig. 3A). Fitting a von Bertalanffy growth model to the relationship between body mass and age (Pitcher and Hart, 1982) resulted in a relationship not significantly different from that reported in Katz and Gosline (1992) for a similar series of individuals (F_s=9.18×10^{-5}, d.f.=1,76, P>0.05). Ground reaction force also increases in a logistic manner, although more slowly, and it does not begin to level off until after the moult into adulthood (Fig. 3B). A similar growth model fitted to the data on ground reaction force results in a period of exponential increase in force that is less than half of that for body mass [$(e^{-0.057x})_{mass} > (e^{-0.019x})_{force}$, where x is age in days, F_s=14.808, d.f.=1,86, P<0.05]. This is manifest in a relatively rapid increase in body mass occurring around an age of 20 days, while the force increases rapidly around day 30. This 7- to 10-day lag between the age of rapid increase in mass and the age of rapid increase in force means that normalizing force by body mass produces a U-shaped relationship between acceleration and age (Fig. 3C).

To analyze allometric relationships we have employed log transformations to convert curvilinear, exponential relationships into linear ones. This has allowed the convenient

comparisons of the scaling exponents that have been transformed into characteristic slopes. Data from individuals on the first day of each instar seemed to be systematically distinct from the rest of the data from that instar. It would seem to be the result of the
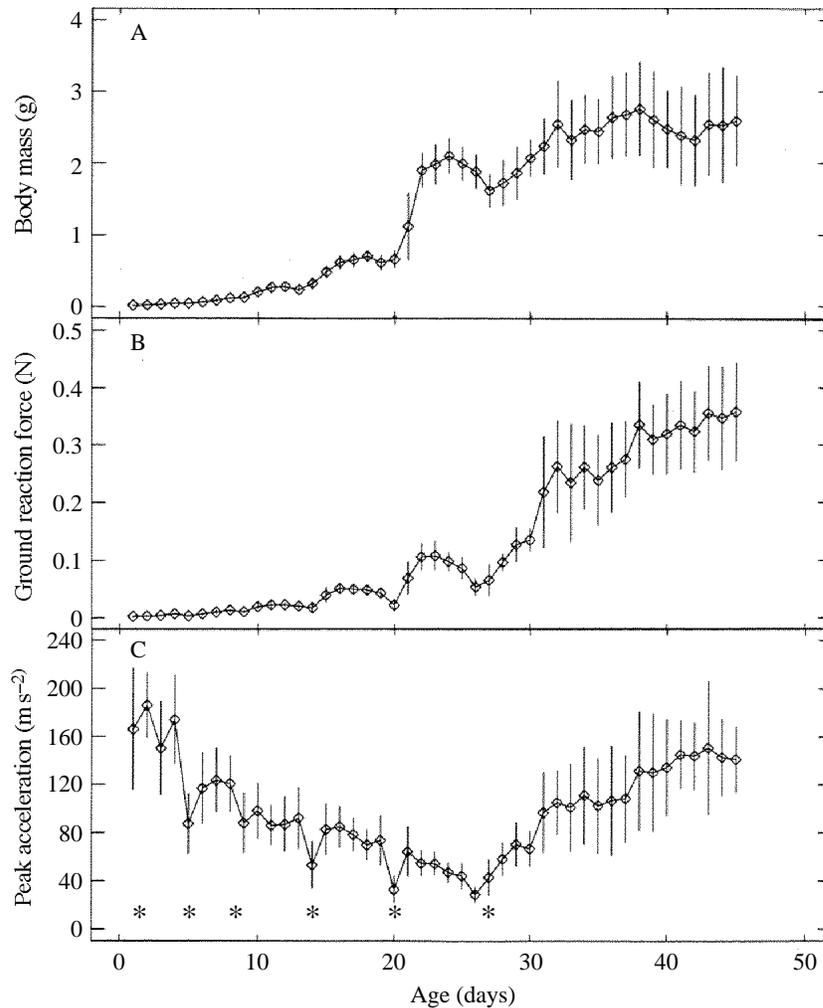

Fig. 3. (A) The relationship of body mass to the age of the locust. Data are reported as means and standard errors of the mean in all three parts of this figure. A regression fitted to the Von Bertalanffy relationship produced the following description of the data: mass=$3.468(1-e^{-0.059x})^3$ (F_s=927.8, d.f.=2,43, r^2=0.937), where x is age in days. (B) The relationship of measured ground reaction force to the age of the locust. A regression fitted to the Von Bertalanffy relationship produced the following description of the data: force=$2.141(1-e^{-0.019x})^3$ (F_s=964.0, d.f.=2,43, r^2=0.955). (C) The relationship of peak acceleration to the age of the locust. These data are reported as means and standard errors of the means for the peak acceleration achieved within individual jumps rather than simply dividing the values in B by those in A. The means are based on a maximum of five jumps from each of five individuals measured on each day. Asterisks denote data from individuals on the first day following a moult.

physiological events involved in moulting that also result in low cuticular stiffness and resilience immediately after moulting (Hepburn and Joffe, 1974; Katz and Gosline, 1992). To prevent the transient events of cuticular stiffening from biasing the regressions, and to make comparisons between data collected from individuals that we believe to be functionally similar (Katz and Gosline, 1992), data from individuals on the first day of each instar were excluded in calculating the slopes of the scaling relationships.

The relationship between log of peak ground reaction force and log of body mass (Fig. 4A) shows a relatively linear region from the smallest individuals up to the fifth instars, but adults fall above this relationship. The regression of the log of peak force on the log of body mass, including both juvenile and adult data, produced the relationship: logforce=0.914logmass+1.678   ($\text{S.E.}=9.89\times10^{-3}$, $r^2=0.877$). The slope of this relationship appears to be similar to that reported for *Locusta migratoria* (Scott and Hepburn, 1976). However, an analysis of variance of the residuals showed a significant lack of fit ($F_s=22.6775$, d.f.=1,260, $P<0.05$), and the regression was deemed an inappropriate description of the data (Draper and Smith, 1981). The regression of the data consisting entirely of flightless juveniles has a slope of 0.732 ($\text{S.E.}=7.89\times10^{-3}$, $r^2=0.925$) and ranges from a low value of 1.99mN on the first day of emergence from the egg to a high of 166mN in fifth-instar individuals.

The relationship in Fig. 4B between log of peak acceleration and log of body mass demonstrates an apparent functional relationship over the first five instars, but a pronounced increase in performance in adults. The values range from approximately 25 $\textbf{\textit{g}}$ in first instars to about 5–7 $\textbf{\textit{g}}$ in fifth instars. The data at larger sizes where the accelerations are once again in the 20–25 $\textbf{\textit{g}}$ range are composed entirely of winged adults. As in the relationship between force and mass, a significant, non-random distribution of the residuals in the regression of log of acceleration on log of mass for the entire data set ($F_s=22.7327$, d.f.=1,260, $P<0.05$) made this an inappropriate description of the data. As such, the regression of acceleration on body mass was performed only on flightless, juvenile individuals. The relationship had a slope of -0.269 ($\text{S.E.}=7.72\times10^{-3}$, $r^2=0.623$).

As the animals grow the duration of the force impulse increases in length from a low value of 12ms in first instars to a high value of 65ms in fifth instars, before falling to 20–30ms in adult locusts (Fig. 4C). These data also show a consistent relationship over the first five life history stages before an inflection at the transition to adulthood. The regression of the log of jump impulse duration on the log of body mass, over the flightless portion of the life history, had a slope of 0.277 ($\text{S.E.}=4.18\times10^{-3}$, $r^2=0.857$), which, while opposite in sign, is not significantly different in magnitude from the slope of the relationship between acceleration and body mass ($t_s=2.913\times10^{-8}$, d.f.=1,470, $P>0.05$). This means that as the animals grow through the first five instars they produce lower accelerations, but they develop that acceleration over a longer time.

By compensating for falling accelerations with increasing impulse durations, juvenile instars produce roughly the same take-off velocity in the jump regardless of age or size (Fig. 5). The flightless, juvenile instars leave the ground at approximately 1.2–1.3 ms^{-1}, while the adults achieve about 2.5 ms^{-1}. The values for adults show good agreement with the value of 2.63 ms^{-1} based on the jump distance of a 3g female locust estimated by Bennet-Clark (1975). For juveniles, the regression of the log of take-off velocity on the
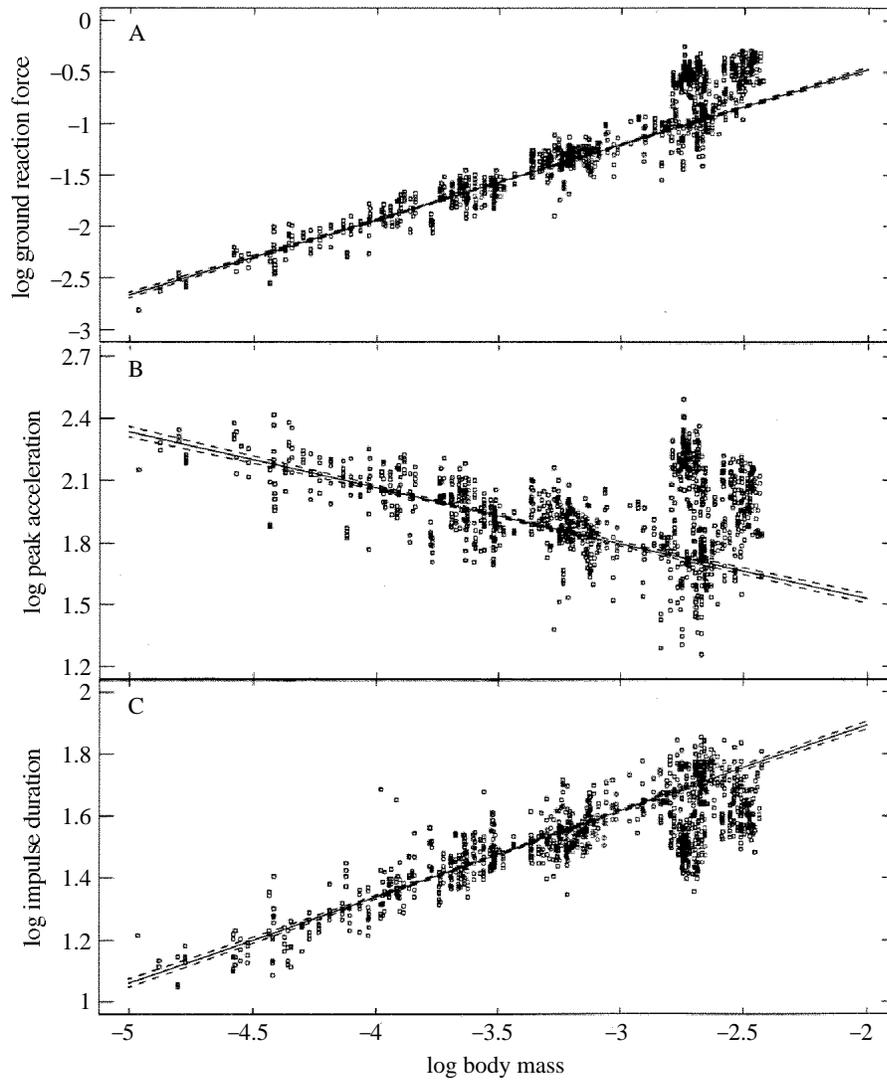
Fig. 4. (A) The relationship between the log of peak ground reaction force (N) and the log of body mass (kg). Each point is the result of one recorded jump like that shown in Fig. 2. These data exclude points collected from individuals on the first day after each moult. The equation for the regression calculated for juvenile individuals is $y=0.992+0.732x$ ($F_s=9045.75$, d.f.$=1,735$, $r^2=0.9249$). The dashed lines are the 95% confidence limits of the regression line. (B) The relationship between the log of peak acceleration (m s^{-2}) produced in each jump and the log of body mass (kg). The equation of the regression line calculated for juvenile individuals is $y=0.989-0.269x$ ($F_s=1213.52$, d.f.$=1,735$, $r^2=0.6228$). The dashed lines are the 95% confidence limits of the regression. (C) The relationship between the log of jump impulse duration (ms) and the log of body mass (kg). The equation of the regression line calculated for juvenile individuals is $y=2.448+0.277x$ ($F_s=4409.27$, d.f.$=1,735$, $r^2=0.8571$). The dashed lines are the 95% confidence limits of the regression.

log of body mass has a slope of 0.053 (s.e.=5.25×10^{-3}, r^2=0.138) (Fig. 5B). While this slope is statistically different from zero (t_s=10.832, d.f.=736, P<0.05), it only resulted in a 21% increase in take-off velocity over the 170-fold range of body mass covered in the juveniles. In the adults the accelerations produced are as high as those produced by the first instars, but the legs are approximately five times as long (Katz and Gosline, 1992), so
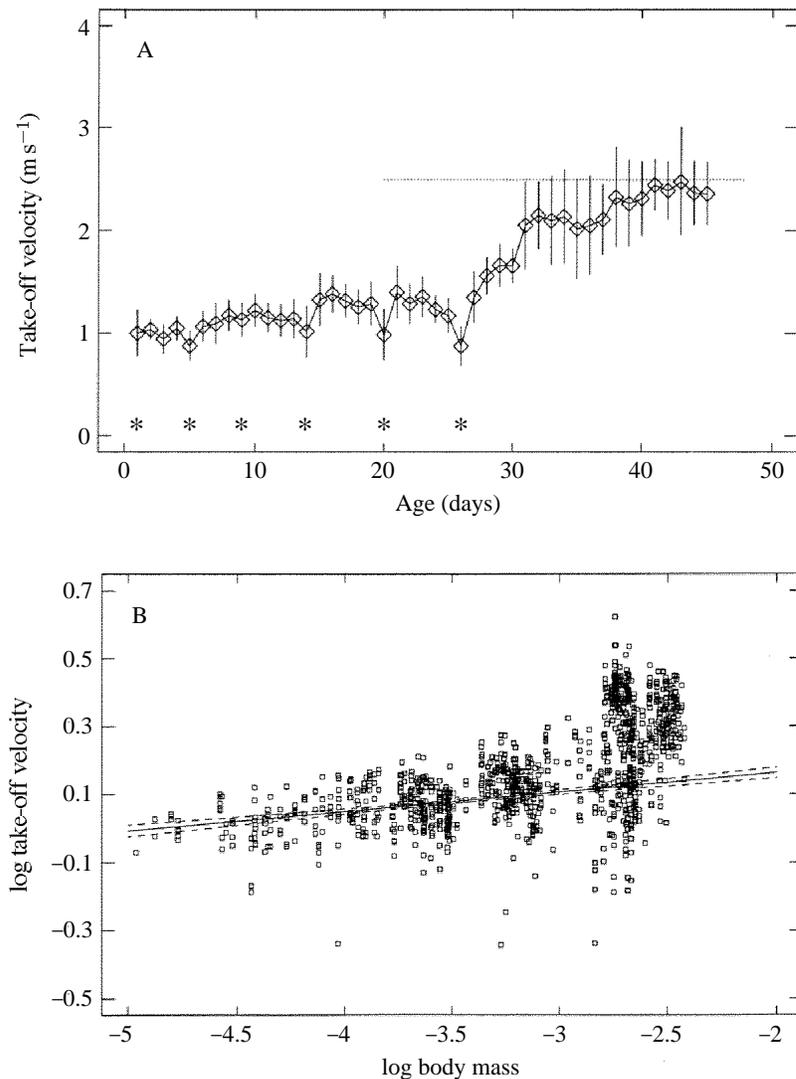

Fig. 5. (A) The relationship between velocity produced in the jump and the age of the locust. Data are reported as means and standard errors of the mean. The first day of each instar is marked with an asterisk. The dotted horizontal line marks the $2.5\,\mathrm{m\,s^{-1}}$ minimum flight speed observed by Weis-Fogh (1956). (B) The relationship between the log of velocity produced in the jump ($\mathrm{m\,s^{-1}}$) and the log of body mass (kg). The equation of the regression line calculated for juvenile individuals is y=0.277+0.056x (F_s=117.33, d.f.=1,735, r^2=0.1377). The dashed lines are the 95% confidence limits of the regression line.

both the acceleration distance and the impulse duration are greater than in first instars. As a result, the take-off velocities are about double those of the previous instars (Fig. 5A). Observation of newly moulted adults indicated that for several days they do not fly. They spend their time hanging from vertical surfaces basking or flapping their wings without leaving the ground. It may be that their wing cuticle requires some time to dry and harden before it becomes sufficiently stiff to provide adequate lifting surfaces. Alternatively, the observation that they are flightless for several days into the adult stage may reflect the fact that relatively low velocities are achieved in the first 6 days of adulthood compared with those after day 30.

The kinetic energy of the jump, calculated at the end of the jump impulse, follows a similar time course to force production, with a large increase in energy in the adult stage (approximately day 30) compared with the juvenile stages (Fig. 6A). The values ranged from a low of 0.004mJ in a first-instar locust to a high of 15.99mJ in an adult. The time course of jump energy within the fifth instar follows a semi-parabolic trajectory, where the energy production is similar on the first and last day of the instar. This is similar to that described for the sixth instar in *Schistocerca americana* (Queathem, 1991). However, none of the earlier instars shows this time course. In the fourth instar of *S. gregaria*, the energy rises on the first 2 days of the instar and then levels off for the remainder. It may be that the more rapid development in *S. gregaria* relative to *S. americana* (approximately 35 days to sexual maturity *versus* approximately 60 days, respectively) and the shorter time spent within each instar mask the changes in the cuticular energy transmission mechanisms to which Queathem attributes the changes in performance that she observed. The scaling relationship between log kinetic energy and log body mass had a form similar to that for force and mass (Fig. 4A). The regression of the relationship for juvenile instars had a slope of 1.114 (S.E.=0.011, r^2=0.939), which is significantly different from a slope of 1.0 (t_s=10.831, d.f.=735, $P<0.05$). The adult locusts produced approximately four times as much kinetic energy as the regression for juveniles would have predicted for animals of adult body mass.

Power developed during the jump follows a time course similar to that for force production (Fig. 7A). This is not surprising as power is the product of force, which follows a sigmoid time course, and velocity, which is relatively constant at the separate juvenile and adult levels. The values for peak power output range from 1.105mW in first instars to 1.379W in adults. The values for average power output in the jump impulse are about one-third of the peak values. For the juvenile instars, peak power output scaled to body mass raised to the 0.772 power (S.E.=0.014, r^2=0.836). Values for average power output scaled to body mass raised to the 0.830 power (S.E.=0.014, r^2=0.862). The difference in these slopes is significant (F_s=8.578, d.f.=1,1136, $P<0.05$) and represents a subtle change in the shape of the force production envelope with increasing peak acceleration, as mentioned above.

By normalizing the power output of the jump by the amount of jumping muscle, we can calculate the specific power output of the jumping muscles and estimate the degree to which elastic energy storage must be employed to amplify the maximal muscular power output of approximately $450\,W\,kg^{-1}$ of muscle (Bennet-Clark, 1975). Gabriel (1985*a*) has published values for the proportion of body mass that is femoral, jumping muscle in

the locust. She highlighted a 50% increase in relative muscle mass between the fourth instar and adult stages. However, she did not specify the age within the instar that these values represent. Additionally, there is quite a lot of variation in the values for relative muscle mass in the juvenile instars, from a high value of 6.1% in first instars to a low of 4.3% in the fourth instars, with no clear temporal trend. For these reasons we have chosen to average her values for all of the juvenile instars to produce a value of 5.56% of whole-
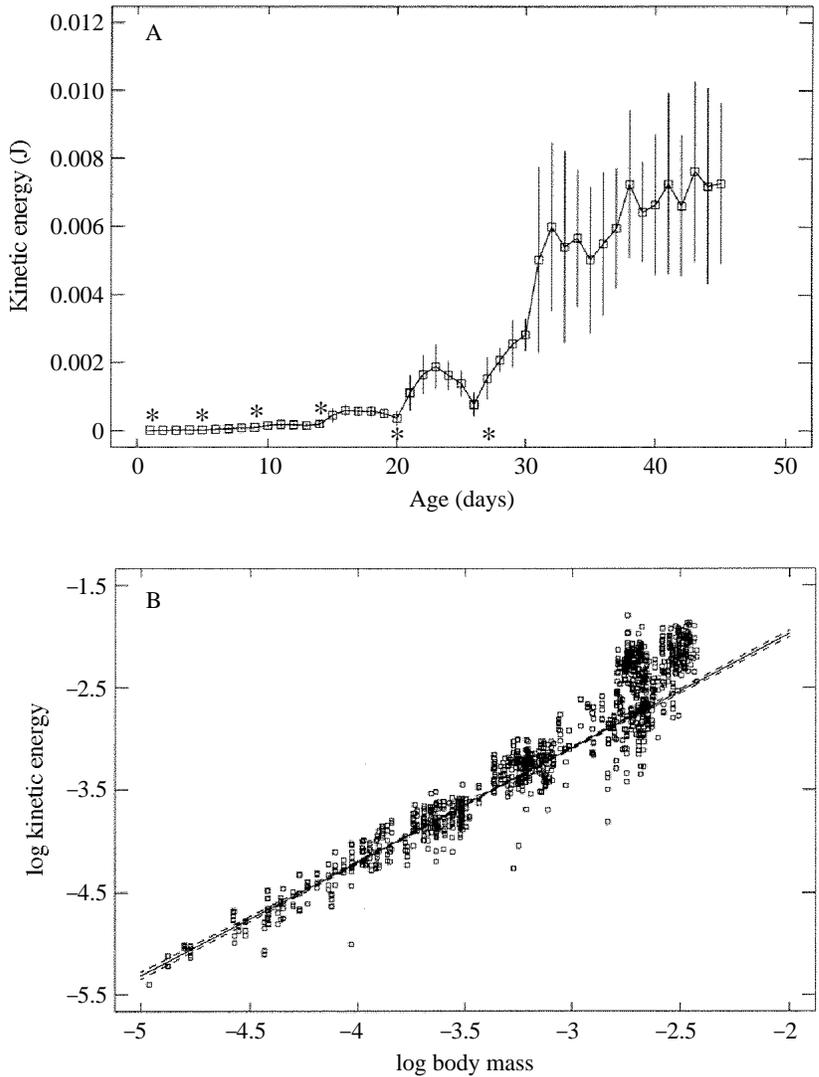

Fig. 6. (A) The relationship between kinetic energy produced in the jump and the age of the locust. Data are reported as means and standard errors of the mean. The first day of each instar is marked with an asterisk. (B) The relationship between the log of kinetic energy produced in the jump (J) and the log of body mass (kg). The equation of the regression line calculated for juvenile individuals is $y=0.253+1.114x$ ($F_s=11238.60$, d.f.=1,735, $r^2=0.9386$). The dashed lines are the 95% confidence limits of the regression line.

body mass that is jumping muscle for all five juvenile instars, and use her value of 6.3 %
for adults.

The daily averages for peak specific power output range from a low of $850 \, \text{W kg}^{-1}$ of
muscle in fifth instars to a high value of $5200 \, \text{W kg}^{-1}$ in the adult stage (Fig. 8A).
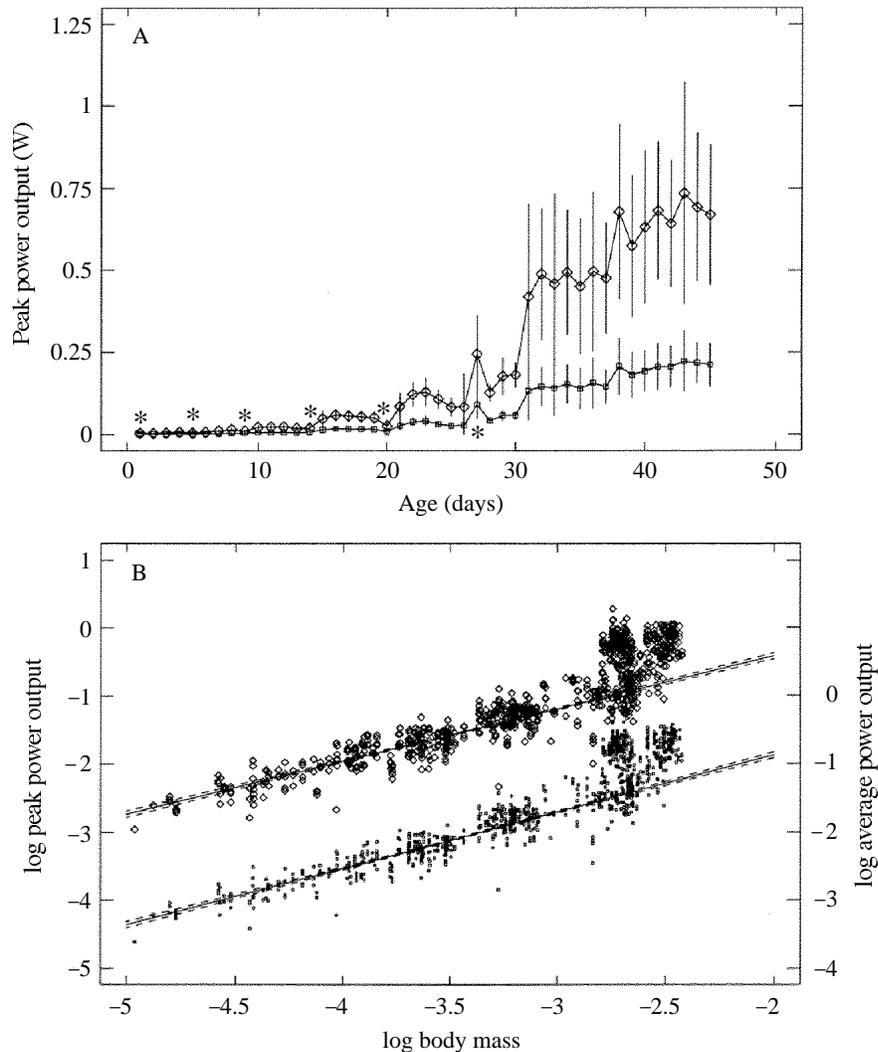However, individual jumps had values as high 11600 and as low as $250 \, \text{W kg}^{-1}$. These

Fig. 7. (A) The relationship of peak power ($\diamond$) and average power ($\square$) produced in the jump
to the age of the locust. Data are reported as means and standard errors of the mean. The first
day of each instar is marked with an asterisk. (B) The relationship between the log of peak
power ($\diamond$) and average power ($\square$) produced in the jump (W) and the log of body mass (kg).
The equation of the regression line calculated for peak power for juvenile individuals is
$y=1.126+0.772x$ ($F_s=2900.77$, d.f.=1,569, $r^2=0.8360$). The equation of the regression line
calculated for average power for juvenile individuals is $y=0.787+0.830x$ ($F_s=3546.39$,
d.f.=1,569, $r^2=0.8617$). The dashed lines are the 95% confidence limits of the regression line.

data agree well with those estimated by Gabriel (1985*a*) based on distance travelled in jumping. They also suggest that on occasion the power outputs of the jump (250 W kg^{-1}) are well within the range for maximal muscle power output (450 W kg^{-1}, Bennet-Clark,
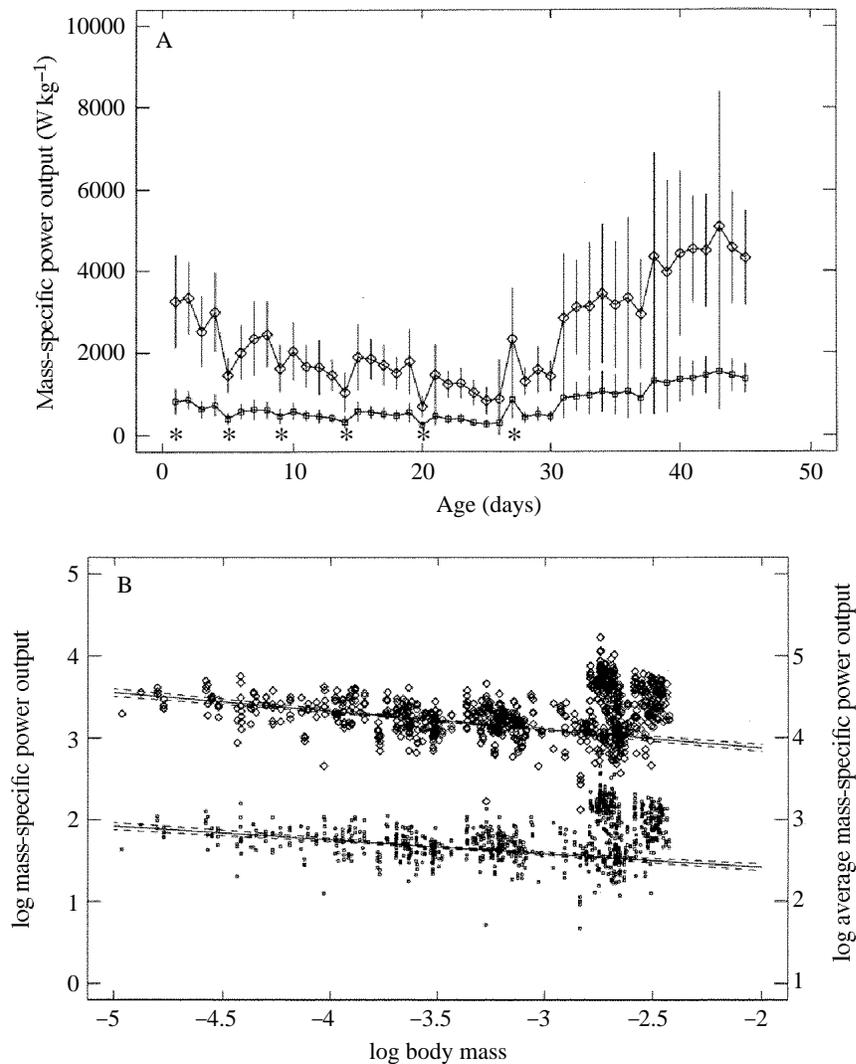

Fig. 8. (A) The relationship of peak mass-specific power ($\diamond$) and average mass-specific power ($\square$) produced in the jump to the age of the locust. Data are reported as means and standard errors of the mean. The first day of each instar is marked with an asterisk. (B) The relationship between the log of peak mass-specific power ($\diamond$) (Wkg^{-1}) and average mass-specific power ($\square$) produced in the jump and the log of body mass (kg). The equation of the regression line calculated for peak mass-specific power for juvenile individuals is $y=2.417-0.228x$ ($F_s=253.69$, d.f.=1,569, $r^2=0.3084$). The equation of the regression line calculated for average mass-specific power for juvenile individuals is $y=2.079-0.170x$ ($F_s=148.09$, d.f.=1,569, $r^2=0.2065$). The dashed lines are the 95% confidence limits of the regression line.

1975). Average mass-specific power output mirrors the data for peak power output at values approximately one-third lower. If a trend exists, it seems that the specific power output declines from a relatively high value in the first instars down to the fifth instars before rising to the highest levels in the adults. For the juvenile instars, peak mass-specific power output scaled to body mass raised to the -0.228 power (S.E.=0.014, r^2=0.308) (Fig. 8B). Average mass-specific power output scaled to body mass raised to the -0.170 power (S.E.=0.014, r^2=0.207). These slopes were significantly different (F_s=8.578, d.f.=1,1136, P<0.05) but, as for the analysis above, we feel this difference is a consequence of the shape of the force production envelope.

Biewener (1989) has suggested that larger animals may reduce the bending moments applied to their long bones relative to those in small animals by adopting more upright postures. It is possible that large locusts use different postures immediately before a jump and may go through different kinematic motion during a jump relative to small instars. Such kinematic differences may affect conclusions drawn from morphological and mechanical comparisons. Fig. 9 shows the relationship between the log of centre of gravity movement during the jump impulse and log body mass. This relationship does not seem to show the discontinuity between juveniles and adults seen in the other measures of performance. The regression for the entire data set has a slope of 0.378 (S.E.=3.70×10^{-3}, r^2=0.885), which is not significantly different from the slope of 0.375 for the relationship between the log of tibial length and log body mass for these locusts (F_s=0.0838, d.f.=1,1363, P<0.05) (Katz and Gosline, 1992). This suggests that the distance over which the acceleration is developed is a constant function of leg length regardless of size
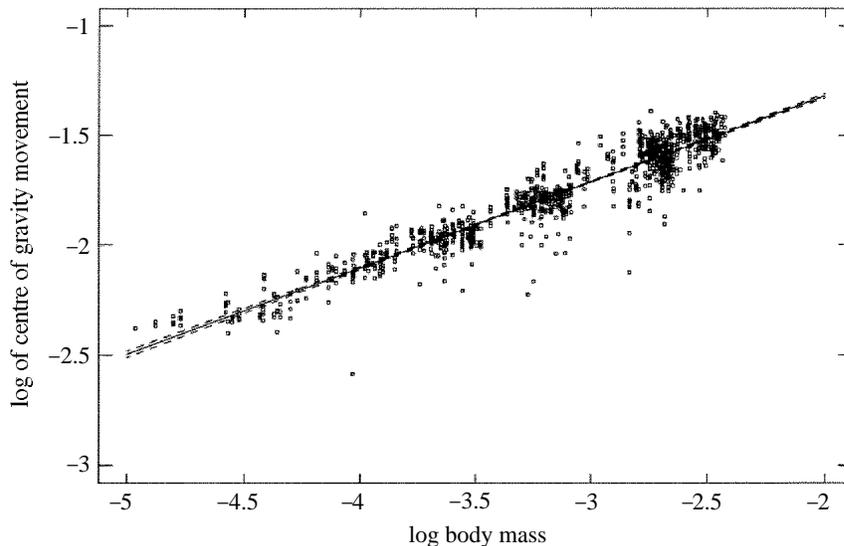

Fig. 9. The relationship between the log of the movement of the locusts' centres of gravity during the jump impulse (m) and the log of body mass (kg). The equation of the regression line calculated for juvenile individuals is $y=-0.676+0.355x$ (F_s=5339.12, d.f.=1,735, r^2=0.8790). The equation of the regression line calculated for all individuals is $y=-0.570+0.378x$ (F_s=10445.36, d.f.=1,1360, r^2=0.8849).

or age. It also suggests that, if the jump impulse starts with the knee joint fully flexed (which seems reasonable based on the anatomy of the catch mechanism, Heitler, 1974), then the jump is kinematically similar in small and large locusts, with no postural scaling. Additionally, any discontinuity in performance at the transition to adulthood, in terms of velocity or acceleration, is not the result of some kinematic or postural feature of the jump mechanism, but is a reflection of changes in the power-generating mechanism.

From ballistics, we can estimate the distance covered by locusts once they leave the ground and become projectiles. Bennet-Clark (1975) presented the following formula to predict the distance covered by a ballistic projectile:

$$d = \frac{v^2 \sin 2\phi}{g}, \qquad (1)$$

where d is the distance covered, v is the take-off velocity of the projectile, ϕ is the angle from the horizontal and g is the acceleration due to gravity. For a constant take-off velocity, therefore, projectiles will cover the same distance over the ground regardless of size. In general it is assumed that projectiles are launched at 45°, which maximizes distance covered for a given take-off velocity. Fig. 10 is a plot of the mean trajectory angle of the jump as a function of age. These data indicate that locusts are capable of taking off at a wide variety of angles. On average, however, they leave the ground at angles between 45° and 55°, but individuals in this study were observed to adjust their trajectories between 15° and 90° to avoid obstacles in their paths. These observations that trajectory angles are highly variable are similar to those of Pond (1972). Given the capability to adjust their trajectory over a wide range, it is difficult to attach much significance to trajectory angles, but in general the trajectories were above 45°. Fig. 11
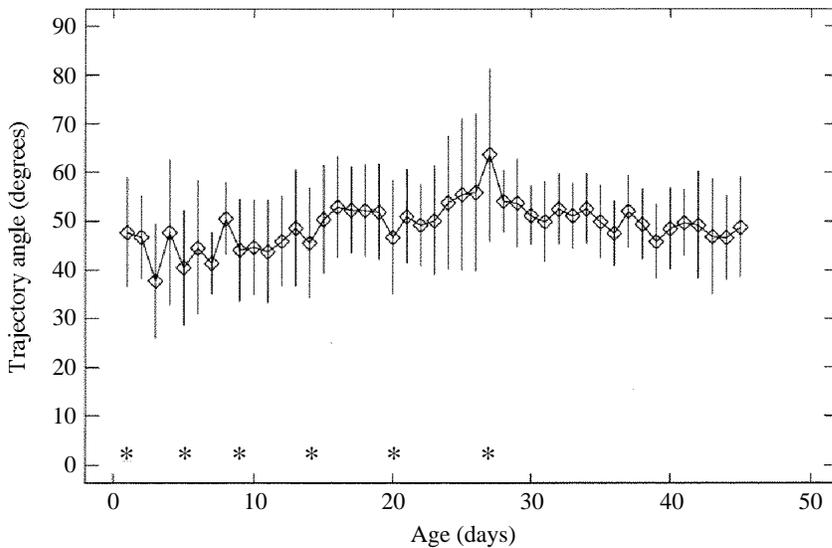

Fig. 10. The relationship between the trajectory angle of the jump and the age of the locust. Data are reported as means and standard errors of the mean. The first day of each instar is marked with an asterisk.
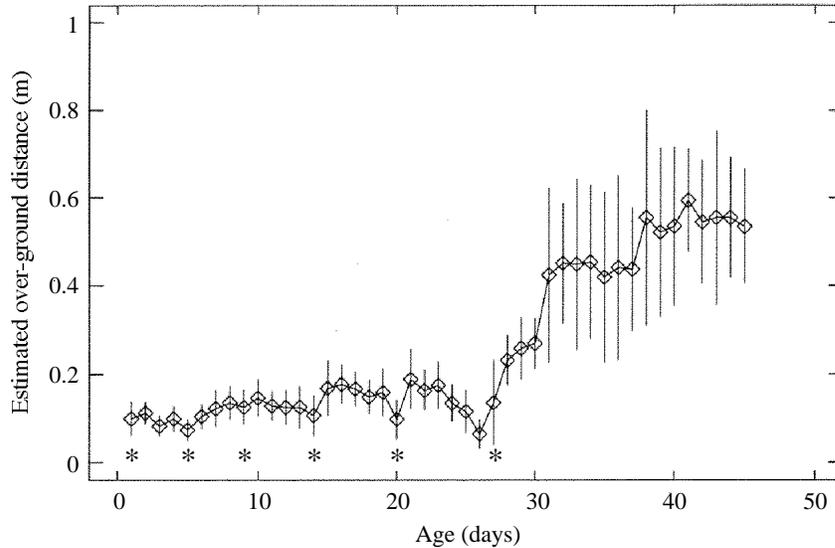
Fig. 11. The relationship between the estimates of the distance covered by the locusts as a ballistic object after they leave the ground and the age of the locust. A description of the calculation of estimated distance is in the text. Data are reported as means and standard errors of the mean. The first day of each instar is marked with an asterisk.

uses the data on trajectory angle, take-off velocity and equation 1 to estimate the jump ranges of locusts on each day that they were tested. The sensitive dependence of distance on take-off velocity is reflected in the relatively constant distance travelled of 15–20cm over the juvenile instars and the threefold increase in jump distance in adults. These values should be viewed as overestimates, especially those for the smaller locusts, because of the kinetic energy losses in overcoming aerodynamic drag once the locust leaves the ground as a projectile (Bennet-Clark and Alder, 1979).

Discussion

Scaling of locomotor performance

The large data set produced here for the jump of these functionally and morphologically similar animals that vary in body mass by more than two orders of magnitude allows us to address questions of how locomotor performance scales in hopping locusts. How might performance parameters such as force, acceleration or velocity scale with body mass? Hill (1950) has provided a rationale for relating morphological dimensions to force, energy and power output by muscles and we have used this rationale to generate quantitative scaling predictions. All of the predicted scaling exponents that are generated, as well as the observed values for *Schistocerca gregaria,* are summarized in Table 1.

If muscle force is the ultimate power plant for the locust jump, accepting the energy storage role of the apodeme and other connective tissue structures (Bennet-Clark, 1975;

Table 1. *Exponents for allometric equations describing both morphological and performance measures from models and those observed for* Schistocerca gregaria

	Model			Observed value for
Scaled parameter	GSM	ESM	CSSM	*S. gregaria*
Morphology				
Limb length	0.333[a]	0.250[a]	0.200[b]	0.377[c]
Limb diameter	0.333[a]	0.375[a]	0.400[b]	0.311[c]
Mechanics				
Flexural stiffness	1.333[c]	1.500[c]	1.600[c]	1.532[c]
Jump performance				
Force	0.667[d]	0.750	0.800	0.732
Acceleration	−0.333	−0.250	−0.200	−0.269
Velocity	0.000[d]	0.000	0.000	0.053
Energy	1.000[d]	1.000	1.000	1.114
Power	0.667[d]	0.750	0.800	0.772
Specific power	−0.333	−0.250	−0.200	−0.288
Movement of centre gravity	0.333	0.250	0.200	0.378

All relationships are modelled by the form $x \propto M^b$, where M is body mass in kilograms. The quantity x is the parameter that is scaled as listed below, and b is the scaling exponent.

[a]McMahon (1973); [b]McMahon (1984); [c]Katz and Gosline (1992); [d]Hill (1950).

GSM, geometric similarity model; ESM, elastic similarity model; CSSM, constant stress similarity model.

Gabriel, 1985*b*), and the force produced by a muscle is a function of its cross-sectional area (Hill, 1950), then we may be able to predict the scaling of force if we know how the muscles' dimensions scale. If we consider a generalized exoskeletal case where the cross section of the muscle is proportional to the square of the diameter of the limb segment that houses the muscle, then we can make predictions about the scaling of force production. In the geometric similarity model (GSM), diameter scales to body mass raised to the 0.333 power (McMahon, 1984). Therefore, force would scale to mass raised to the 0.667 power (i.e. $mass^{0.333} \times mass^{0.333} = mass^{0.667}$), and acceleration would scale to mass raised to the −0.333 power (i.e. $mass^{0.667}/mass^{1.000} = mass^{-0.333}$). The elastic similarity model (ESM), which predicts that diameter will scale to mass raised to the 0.375 power (McMahon, 1973), predicts that force production will scale to mass raised to the 0.750 power, while acceleration will scale to mass raised to the −0.250 power. Similarly, the constant stress similarity model (CSSM), which anticipates diameter scaling to mass to the 0.400 power (McMahon, 1984), predicts mass scaling exponents of 0.800 and −0.200 for force and acceleration, respectively.

Importantly, velocity is predicted to be mass-independent in each model. Velocity in jumping animals is determined by the following relationship (Bennet-Clark, 1977, equation 5):

$$v = \overline{2sa},\qquad(2)$$

where v is take-off velocity, s is the acceleration distance (a function of leg length, above

and Fig. 9) and *a* is the average acceleration produced in the jump. Therefore, we can relate the scaling of velocity to the scaling of leg length and acceleration. For each model, acceleration and leg length have scaling exponents that are equal in magnitude, but opposite in sign. Therefore, their product scales to body mass raised to the zero power and is scale-independent.

Unlike the scaling of velocity, energy is predicted to scale directly with mass raised to the first power but, like the scaling of velocity, it is model-independent. Energy is the product of force, the product of two diameters, and distance, a length. So energy will scale directly with the volume of either the muscle producing the force or the spring that stored the force.

The scaling of power output during the jump can be predicted from the scaling relationships between performance and body mass. Power is the product of force and velocity. As we described above, velocity is predicted to be scale-independent by all models. Therefore, power output in the jump should scale to mass raised to the same power as force is for each model.

So how do the models anticipate the observed relationships for *Schistocerca gregaria*? The observed scaling exponent for the dependence of peak force production on body mass (0.732, Fig. 4A) most closely approximates elastic similarity; however, it proves to be statistically different from ESM's prediction of 0.750 (t_s=2.393, d.f.=735, 0.1>P>0.05). This scaling exponent for force production in locusts is intermediate to that estimated for vertebrate hoppers from anatomical measures. Alexander *et al.* (1981) reported relationships between muscle masses, muscle fibre lengths and body mass for a variety of vertebrate hoppers. In all hindlimb muscles reported, the mass of muscle scaled very close to body mass raised to the first power. By employing Alexander's (1977) method of estimating cross-sectional area of muscle, we estimated that deep hindlimb flexors muscles' fibre areas scaled to mass raised to the 0.65 power (similar to the prediction of geometric similarity), while in the quadriceps group it scaled to body mass raised to the 0.75 power (equivalent to elastic similarity), and in the ankle extensor group it scaled to body mass raised to the 0.80 power (equivalent to constant stress similarity). This suggests that, within the morphological design programme that produces geometrically similar amounts of muscle, these animals are increasing the muscles' force-producing capacity per unit mass. They are presumably accomplishing this by changing the muscle fibre architecture, i.e. increasing pinnation angle of the more distal limb muscles relative to those more proximal. It is tempting to suggest that these animals are adopting a distortive allometry (i.e. ESM) that increases the cross-sectional area of muscle in larger animals relative to small ones in a way that biases the increase towards the distal end of the limb relative to the proximal end. It accomplishes this, however, without increasing the relative mass of muscle at the distal end of the limb, thus preventing an increase in the energetic costs of accelerating and decelerating the limbs during locomotion.

The scaling exponent of peak acceleration as a function of body mass (−0.269, Fig. 4B) also is most consistent with elastic similarity, but again proves to be different statistically from ESM's prediction of −0.250 (t_s=2.471, d.f.=735, 0.1>P>0.05). The fact that the slope of acceleration on body mass differs from the model prediction to the same

extent as does the slope of the relationship between force and mass is not surprising as the acceleration data are normalized force values. Thus, it seems that the relationships between force production and body mass and acceleration and body mass are approximately as predicted by the elastic similarity model. The statistical differences observed may reflect the influence of morphological scaling that produces longer, relatively more slender, legs in larger locusts (Katz and Gosline, 1992). Nevertheless, as observed for the mechanical properties of the tibiae (Katz and Gosline, 1992), the observed performance (i.e. force production) approximates ESM in spite of a morphological programme that deviates rather dramatically from elastic similarity.

All models predict mass independence for scaling of velocity in the jump, but we observed that the velocity scaled to mass raised to the 0.053 power. Where does this difference come from? The predictions are based on assumptions about morphology, but we have previously shown that locust leg lengths scale to mass raised to the 0.377 power, which is larger than any of the models predict (Katz and Gosline, 1992). Equation 2 allows us to eliminate assumptions about morphology and to predict how velocity should scale given the scaling of leg length observed in *S. gregaria*. The square root of the product of acceleration and leg length (equation 2) should scale to body mass raised to the 0.054 power, which is not significantly different from the observed value of 0.053. This explains *how* the scaling of velocity arises, but it does not seem to spotlight a design strategy *per se* that can explain *why* locusts produce relatively more elongate legs as they increase in size. That is, we have no *a priori* reason to anticipate a scaling exponent of 0.05.

The scaling slope of energy output that we observe in juvenile instars (1.114, Fig. 6B) is higher than the models predicted. It may be that the relatively larger output of energy seen in larger juveniles is a result of the increased quality of the material that stores the energy prior to the jump. Before the jump the energy is stored in the extensor apodeme and semilunar process (Bennet-Clark, 1975), and during the jump the energy is transmitted through the metathoracic tibiae to the ground (Brown, 1963; Katz and Gosline, 1992). The cuticular springs form an energy transmission system. Katz and Gosline (1992) showed that the material resilience increases by approximately 20% from the first to the fifth instars. If we assume that this increase in resilience is reflected in all of the cuticular elements and adjust the amount of energy we measure in the jump by the energy loss characteristics of the transmission, we can estimate how much energy was put into the system prior to the jump and how this quantity scales to body mass. The estimated energy input to the transmission scales with body mass raised to the 1.08 power (F_s=10129.02, d.f.=1,735, r^2=0.932), which, while closer, is still statistically different from the prediction of 1.00 (t_s=7.9997, d.f.=735, $P<0.05$).

Whereas each of the other measures of jump performance appears to scale close to the predictions of elastic similarity, peak power output scales to body mass in a manner most similar to the predictions of constant stress similarity (0.800). It does so in a sensible way, however, as it is the product of force, which scales approximately elastically (0.732), and velocity, which scales to a higher exponent than anticipated (0.053). As a result, power outputs scale to body mass in a manner that is intermediate between the predictions of elastic and constant stress similarity (0.772). Because we are calculating the power within

each impulse, the scaling exponent for power and body mass is numerically different from that which might be predicted simply from taking the product of the scaling relationships for force and velocity (i.e. 0.732+0.053=0.785 *vs* 0.772). This difference indicates that the shapes of the force and velocity envelopes contribute to the estimate of power produced in the jump. It also suggests that our examination of the slopes of the energetic relationships are independent; that we are not 'boot-strapping' our data to compare the energy or power output and body mass relationships.

Acceleration and design

Though we have not discussed the data for jump performance in terms of life history strategies, predator avoidance has been the context for previous analyses of jumping in locusts and anurans (Scott and Hepburn, 1976; Emerson, 1978; Queathem, 1991). In each case the suggestion has been made that acceleration produced in the jump is the critical performance parameter. In discussing jumping in anurans, Emerson (1978) used scale independence of jump performance parameters to discriminate models that associated specific measures of performance with success in avoiding predation. She found that in *Rana pipiens* and *Pseudacris triseriata* average acceleration was relatively scale-independent over a 30-fold range in body mass, while *Bufo americanus* showed a decrease in average acceleration with increasing size. By this criterion, the ontogenetic data on locusts suggest that acceleration *per se* is not necessarily the key functional performance feature, but that the velocity developed in the jump is perhaps more important. This suggestion is based on two observations. First, velocity, which is relatively scale-independent over the first five instars, rather than acceleration, which varies fourfold, is regulated by the developmental design programme. While there seems to be a functional relationship between falling accelerations and increasing body mass for juveniles, the duration of force development in the jump seems to be compensating quantitatively for the fall in acceleration to provide a relatively constant take-off velocity. The scale independence of take-off velocity suggests that, if selection has operated on the jump performance of this locust, then velocity, or a consequence of velocity, is the key performance parameter. Second, there seems to be an unexploited potential to improve acceleration performance in flightless instars that is exploited to some extent in adults.

Fig. 12 provides a comparison of the accelerations produced in jumping locusts with published values for the flea *Spylopsyllus cuniculus* (Bennet-Clark and Lucey, 1967), the click beetle (Evans, 1971), the mediterranean fruit fly larva (Maitland, 1992) and the standing jump of the kangaroo rat (Biewener *et al.* 1988). If we perform a two-point regression between the data for the adult flea and an average value for adult locusts (the two animals in the figure that we know jump using similar cuticular spring mechanisms), the slope turns out to be −0.2499. The slope of the relationship between acceleration and mass predicted by ESM of −0.25 would seem to describe the adult fleas and locusts even better than it describes the flightless locusts. The flea, fruitfly maggot and kangaroo rat all produce accelerations that deviate from the prediction made by the juvenile locusts' performance to approximately the same extent as does that of the adult locust. This suggests that the same functional design issues that determine scaling relationships in flightless, juvenile locusts act to determine the separate relationships for adult locusts and
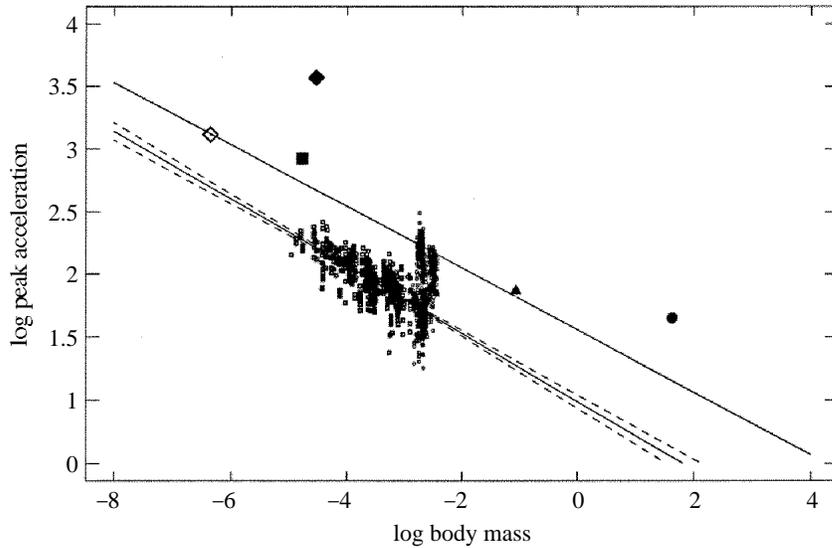
Fig. 12. The relationship between the log of peak acceleration produced in jumping $(m\,s^{-2})$ and the log of body mass (kg). This figure compares the data reported in Fig. 4B with published values from other jumping animals. Data are presented for the flea ($\diamond$), *Spylopsyllus cuniculus*, from Bennet-Clark and Lucey (1967), the click beetle ($\blacklozenge$) from Evans (1971), the mediterranean fruit fly larva ($\blacksquare$) from Maitland (1992), as well as the standing jump of the kangaroo rat ($\blacktriangle$) from Biewener *et al.* (1988) and the continuous hopping of the kangaroo ($\bullet$) from Alexander and Vernon (1975). The equation of the two-point regression made between the data from the flea and the average calculated for all the adult locusts had a slope of -0.2499, which seems indistinguishable from that for the prediction of elastic similarity (-0.250).

these other jumping animals of widely different designs. Apparently the robust predictions of ESM apply to these jumping animals generally, but the juvenile locusts are able to get by (in an evolutionary sense) with about one-third lower accelerations per body mass than the heroic performance of the adults and these other animals.

A feature of these relationships is that, if elastically similar jumping animals increase in size and travel down the line relating acceleration with body mass, there is a point where the accelerations fall to a level where the animal will be unable to leave the ground in a jump, and the body mass where this occurs will be an absolute limit to body size for a given jumping 'design'. Realistically, a functional limit will occur before this point as decreasing accelerations produce slower and shorter jumps, in the absence of spectacular compensatory specializations of leg length to increase the interval over which acceleration is developed. In any event, it seems that an animal that is elastically similar to juvenile locusts could not continue to get larger indefinitely, and for larger animals to jump they must move away from the relationship between acceleration and body mass for juvenile locusts and produce higher accelerations at a given size.

There seem to be two design strategies that could allow an animal to get away from any of these relationships: either produce more force per unit body mass (i.e. increase the proportion of body mass that is jumping muscle) or increase the efficiency of the energy

transmission system in producing ground reaction force. Gabriel's (1985*a*) data on locusts suggest that locusts have increased the proportion of body mass that is jumping muscle to achieve the high accelerations seen in the adults. Gabriel (1984) made the point previously that in larger animals, where energy production capacity limits jumping performance, increasing the relative investment in jumping muscle is the most effective way of improving jumping performance. Clearly 40 kg kangaroos are not 'elastically' similar to adult locusts (Fig. 12), and it has been observed that as much as 8–10% of the body mass is invested in hindleg muscle of a kangaroo (Alexander and Vernon, 1975) compared to 4.5–6% in locusts (Gabriel, 1985*a*). Also, kangaroos are storing kinetic energy from one stride and using it in a following stride while locusts use energy that is stored during the same stride.

It seems significant that the data for standing jumps in kangaroo rats and mediterranean fruit fly larvae lie so close to predictions based on adult locusts and fleas. In both cases the animals use quite different jumping mechanisms from the locust. Indeed, the fruit fly maggot is legless. In continuous locomotion, the kangaroo rat is known to use elastic energy stored from previous strides to increase the accelerations and energy output of a jump (Biewener *et al.* 1981) but, in single jumps from standing starts, they are not known to use stored spring energy. It is therefore interesting to see that the data for a standing jump in the kangaroo rat are so close to the prediction made from adult locusts and fleas (Fig. 12). This relationship may reflect common design features in very different animals. It could be that for a given relative investment in jumping muscle each animal gets a similar acceleration output regardless of morphological design. The limits to this suggestion are demonstrated by both the click beetle, which has a similar investment in muscle as the locust, but much higher relative accelerations ($3800\,\mathrm{ms}^{-2}$, Evans, 1971), and the fruit fly maggot, which has similar accelerations to the locust, but much larger investment in jumping muscle (16%, Maitland, 1992). It remains to be discovered if this relationship, which suggests that these jumping designs are elastically similar, is other than a coincidence.

In going from the line for juvenile locusts in Fig. 12 to the line for adults, the relative muscle mass increases approximately 20%, but the kinetic energy output goes up by fourfold (Fig. 6B). Does the 20% increase in relative muscle mass between fourth instars and adults explain the increase in performance observed at the transition to adulthood? Where might additional energy come from? Gabriel (1985*b*) made the observation that the distance covered as a ballistic projectile increased by 300% between fourth-instar hoppers and adults. She explained that the increased energy produced in the jumps of adult locusts was the product of relatively stronger muscles applying more force to stiffer energy storage devices, and therefore storing more energy. She noted that adult extensor muscles' pinnation angle increased and relative muscle fibre length decreased relative to those of fourth-instar locusts, indicating that the muscle was capable of producing more force per unit volume. She also showed that the adult apodeme increased in cross-sectional area by 440%, presumably increasing in stiffness relative to that of the fourth-instar hoppers, and the semilunar process increased in measured stiffness by sixfold (Gabriel, 1985*b*). She felt that the increased stiffness of the spring combined with the increased force output of the muscles could account for a large part of the increase in

specific energy seen in the jumps of adults. This analysis, however, does not seem to describe the situation in locusts adequately. Gabriel reports the functional cross section of the tibia extensor muscle as $5.7mm^2$ and $18.9mm^2$ for the fourth instar and adult, respectively. When the area is normalized by the body mass being accelerated, the values are the same for the different age classes ($20.40mm^2 g^{-1}_{4th\ instar}$ vs $20.58mm^2 g^{-1}_{adults}$). Similar forces applied to more easily deformed springs could also store relatively larger amounts of energy, but this also does not appear to be the case. Gabriel's data show that the force-producing cross-sectional area of muscle is applied to a relatively larger cross-sectional area of apodeme in the adults compared to the fourth instars ($1781mm^2 muscle mm^{-2} apodeme_{4th\ instar}$ vs $1092mm^2 muscle mm^{-2} apodeme_{adults}$). This results in the apodeme springs seeing 37% less force per unit spring area in adults. What we have, therefore, are similar forces applied to relatively stiffer springs, resulting in smaller deformations of the springs and smaller amounts of energy stored in adults relative to fourth instars. We are still left wondering where the additional energy comes from in the adults' jumps. It seems very likely that Gabriel's suggestion that the juvenile muscles are not working as hard as they are in adults is correct (Gabriel, 1985*a,b*; Gabriel and Sainsbury, 1982).

The ontogenetic role of jump performance

Bennet-Clark (1977) showed how body size plays an important role in jumping design. Chiefly, this results in the jumps of small animals being limited by their ability to generate power output, while the jumps of larger animals are limited by their ability to generate kinetic energy. Gabriel (1984) analyzed these ideas and predicted that small, power-limited animals can achieve better performance either by getting larger or by increasing their leg length. In the largest jumpers she felt that improvements in performance could optimally be achieved by increasing the fraction of the body mass that was committed to jumping muscle. Indeed, she reported that, across the ontogenetic increase in body mass in locusts, jump performance improved by increasing body size up to the size of fifth instars. In adults, however, jump performance was improved by increasing the relative mass of jumping muscle by approximately 50% over that in fourth instars (Gabriel, 1985*b*).

Our results indicate that the increase in jump performance seen in adults does not represent a change associated with body size, but rather a change in life style. It is no mere coincidence that the increase in jumping muscle occurs at a time when the mode of locomotion switches from hopping to flying. We suggest that a single strategy may not appropriately describe the development of jump performance. Rather, it may be more reasonable to develop one framework to analyze the juveniles and another to analyze the adults; frameworks that are constructed to account for what may be entirely different ecological roles of the jump at different points in the life history. In small locusts we see an increase in leg length that is rapid relative to the increase in body size (Katz and Gosline, 1992) as a strategy for increasing jump performance. The increase in jumping performance in adults reflects a switch to flight and the demand that flight makes for higher-performance jumps. Indeed, this distinction has already been alluded to in discussing locust jump performance data (Scott and Hepburn, 1976; Gabriel, 1984;

Queathem, 1991). This interpretation seems fundamentally different from the switch to larger investment in jumping muscle mass in larger jumping animals that Gabriel (1984) anticipates. If we were keen to shoe-horn our observations into Gabriel's paradigm, then we might say that the locust exploits the increasing leg length strategy up to the point where the locomotor strategy changes and there is a demand for a fundamentally different, and stronger, jump. If this represents a strategy, then we view it as a locomotion mode change issue, rather than a body size issue *per se*.

The ontogenetic increase in body mass and increase in peak force production are the result of a clear difference in developmental timing. The relatively early period of rapid mass increase would seem to indicate that for young, small locusts getting larger is a higher priority than increasing force production to maintain high accelerations in the juvenile instars. Once the locusts have achieved a large adult mass, the delayed period of rapid increase in force production results in relatively high forces that produce large accelerations quantitatively similar to those observed in first-instar individuals.

Acceleration is dependent on the amount of force produced by the jumping muscles and the body mass being accelerated. So the adults are producing 25 *g* of acceleration by producing more force per unit body mass than the flightless fifth instars of similar body mass (Fig. 12). If survivorship required as high acceleration performance as possible, then why wait until adulthood to increase the force output of the jumping machinery? It seems that the high acceleration per body mass seen in adults could be achieved in juveniles with benefits to predator avoidance by advancing the developmental timing of jumping muscle growth. Certainly it has not been necessary to invoke predator avoidance as a 'strategy' for the jump in the flea. Therefore, having high peak acceleration as a strategy for predator avoidance seems questionable. If the jump of the locust produces one velocity, and therefore distance, in flightless individuals, and another velocity in winged ones, what is significant about these two levels of performance? In flightless, juvenile instars the jump data predict a distance travelled of approximately 20cm, a figure that is intermediate between the maximum performance of 30cm and average of 11–14cm for fourth and fifth instars observed by Gabriel (1985*a*). Regardless of the specific distance, the interpretation is the same: there appears to be a functional distance that is important to the hopping locust. To test this hypothesis it would be important to look for some characteristic dimension in the locust's environment that correlates with the jump distance. It may be that there is a pattern to the spacial organization of the vegetation that forms the food source for the hoppers that has a characteristic spacing of 20–30cm.

In adults, the important parameter may not be distance travelled, but rather take-off velocity itself. It is significant that the twofold increase in take-off velocity occurs at the time in the life history when the primary mode of locomotion switches from hopping to flying. Weis-Fogh (1956) reported that locusts flying in wind-tunnel experiments stop flying when the wind speed falls below 2.5 ms^{-1}. It seems unlikely that the minimum observed flight speed and the take-off velocity in adults are the same is simply a coincidence. Because locusts use unsteady-state aerodynamics during take-off, it is difficult to estimate what their minimum flight speed might be *a priori*. However, it seems reasonable to estimate what effect the increased take-off velocity might have on

thrust production using actuator disc theory. With actuator disc theory, we need not be specific about the anatomy or the mechanics of the thrust-generating mechanism. For actuator discs, the thrust produced is proportional to the mass flux of fluid moving through the actuator times the velocity of the fluid. The quantitative relationship is:

$$T = \rho S_d v[V + (v/2)], \qquad\qquad (3)$$

where T is the thrust produced by the actuator-disc, ρ is the density of the fluid, S_d is the disc area (calculated as a circular disc swept out by wings of a known length), V is the forward velocity of the actuator relative to the fluid and v is the increment of velocity added to the fluid as it passes through the actuator disc (Blake, 1983). Fig. 13 is a plot showing real solutions of equation 3 for v in terms of varying values of V. The data in Fig. 13 suggest that as the actuator disc moves through the fluid at higher velocities (V), the increment of additional velocity (v) falls rather quickly. For a 3.2g female locust with 5.5cm long wings to take off from a standing start, the wings must generate an air-flow of
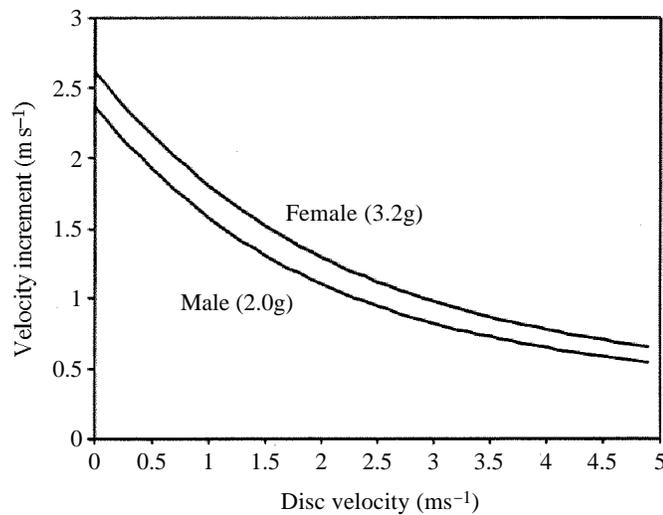

Fig. 13. Increment of additional velocity required to produce thrust for actuator discs moving at various velocities. The data are solutions for the equation 3 in the text relating thrust produced by an actuator disc to the velocities of the fluid moving through the disc. The magnitude of the force vector oriented at 55° to the horizontal whose downwardly resolved component was exactly equal to the body weight of the locust was chosen as the minimum thrust required for the jump. A body mass of 3.2g, a wing length of 5.5cm and a density of air of $1.1746 \, kg \, m \, m^{-3}$ were used to calculate the data labelled Female in the figure. A mass of 2.0g and a wing length of 4.8cm were used to calculate the data labelled Male in the figure. The data indicate that producing $2.5 \, ms^{-1}$ in the jump of a 3.2g female requires the production of 35.6% less additional velocity going through the disc, and 73.3% less power required, relative to an end-jump velocity of $1.1 \, ms^{-1}$. The data also indicate that jumping at $2.5 \, ms^{-1}$ requires 57.2% less additional velocity than a standing start with a power requirement savings of 92%. The estimates for the smaller, male locusts suggest that the increase to adult take-off velocities lowers the additional velocity required by 37.5% and reduces the power required for take-off by 75.6% over the requirements imposed by the juvenile end-jump velocities.

$2.62\,\mathrm{ms}^{-1}$ to generate sufficient thrust to balance body weight. By jumping off the ground at $2.5\,\mathrm{ms}^{-1}$ at an angle of 55° to the horizontal, the additional velocity that the wings must generate falls to $1.12\,\mathrm{ms}^{-1}$ – a decrease of 57%. Were the adults to reach the same end-jump velocity as the fifth instars, the wings would have to generate a flow through the disc of $1.74\,\mathrm{ms}^{-1}$, a decrease of only 33% over a standing start and 55% greater than the increment of velocity for a jump of $2.5\,\mathrm{ms}^{-1}$. For a 2g male with 4.8cm long wings the data in Fig. 13 suggest that jumping with a velocity of $2.5\,\mathrm{ms}^{-1}$ requires an additional increment of velocity of $0.95\,\mathrm{ms}^{-1}$, a reduction of 60% from the standing-start disc velocity of $2.37\,\mathrm{ms}^{-1}$. Since the power required by an actuator is proportional to the third power of the disc velocity (Von Mises, 1959), the difference in end-jump velocities between fifth instars and adults represents a 75.6% saving in power required to generate the thrust necessary to overcome the force of gravity. This power saving seems considerable, but without knowing explicitly what the power requirements are for flying at $1.1\,\mathrm{ms}^{-1}$ relative to the maximal power output capacity of the flight muscle it is impossible to say whether the jumping velocity developed by juveniles represents an absolute limit to flight by locusts. Alternatively, it may be that to jump much faster requires uneconomically high jumping muscle power output and the observed jumping velocity represents a balance between the falling demands for power from the flight muscle and the increasing demands for power from the jumping mechanism with increasing end-jump velocity.

These observations suggest that achieving a high take-off velocity for the initiation of flight has demanded a higher-performance jump than could be provided by the force production of the juveniles, and we believe that this increased demand for performance is the design issue that has driven the increase in power output in the jumps of adults over those of juveniles.

Conclusions

In the case of each measure of performance that we can directly relate to morphological predictions (i.e. force, acceleration, energy production, velocity), the predictions of elastic similarity are approximated. In the case of power output and specific power output, which scale in a manner more close to constant stress similarity, the observed scaling for *S. gregaria* is quantitatively reasonable based on the dependence of power output on the other performance characteristics. However, the approximation of elastic similarity is achieved in spite of a morphological design programme that deviates dramatically from elastic similarity. The scaling relationship between acceleration and body mass that is predicted by elastic similarity seem remarkably robust in that data from a variety of animals, including invertebrate and vertebrate hoppers, follow the same scaling relationship as that for adult fleas and adult locusts.

The jump of the locust has different functions in the flightless, juvenile stage and in the flying adult stage of the life history. It seems that juveniles are designed to achieve a functional velocity of 1.2–$1.3\,\mathrm{ms}^{-1}$ at the end of the jump impulse, which produces a characteristic distance of 20–30cm covered as a ballistic object. The adults are producing approximately twice as much velocity in the jump to achieve a minimum characteristic velocity of $2.5\,\mathrm{ms}^{-1}$ for the initiation of flight. This change in functional role of the jump

is reflected in abrupt discontinuities in the scaling relationships for force, acceleration, velocity, energy and power production as functions of body mass.

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