

Variation in jump force production within an instar of the grasshopper *Schistocerca americana*

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(With 6 figures in the text)

Jumping ability varies by two-fold within an instar during the moult cycle in the grasshopper, *Schistocerca americana* (Acrididae: Cyrtacanthacridinae). Changes in jump distance could result from deviations in jump angle away from the optimum during development, a change in jump energy and/or a change in body mass. Body mass has already been shown to vary by over two-fold within an instar (Queatham, 1991). In the present study, jump angle remained near the optimum of 43° during the time course of maximal jumps throughout the instar. Jump energy was correlated with ground reaction force production because energy lost to backward rotation and drag was small. Ground reaction force production varied by nearly four-fold over the period of the instar. Within instar six, force production and body mass accounted for 85% of the variation in jump distance. Their patterns of change relative to one another explain the four functional stages we define for within instar performance. Jump distance increased early within instar six (Stage I, days 0–2) because force production increased. In Stage II (days 3–8), jump distance remained at its peak because an increase in body mass was offset by an equal increase in force production. Jump distance decreased in Stage III (days 8–11) because body mass continued to increase while force production levelled off. Force production decreased to a greater extent than body mass during Stage IV (days 11–13), resulting in a further decline in jump distance during the three days preceding the moult to adulthood. Our results suggest that further examination of the musculo-skeletal system could provide a causal explanation for this change in jumping ability within an instar. The present study illustrates the remarkable physiological and mechanical changes that affect locomotion within a single instar, and highlights developmental differences between arthropods and vertebrates. Arthropod development is by its very nature a discontinuous process separated by periods of continuous, parabolic changes, and this pattern of growth is reflected in locomotor performance through ontogeny.

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Introduction

In the animal kingdom, two groups have evolved the ability to run, jump, swim and fly. Both vertebrates and arthropods begin life small, like most other organisms, and acquire resources over time to increase in size before reproduction. Vertebrates can increase in size continuously, but arthropods must undergo a series of moults separating discrete developmental stages, or instars. Although size is recognized as probably the single most important attribute of any organism, few studies analyse in detail how locomotor performance changes as animals grow.

The study of how moulting affects locomotion demands mechanically well-defined locomotor behaviour. Jumping is a locomotor mode whose modelling takes advantage of ballistics theory. This theory describes how the distance travelled by a projectile will vary with the mass of the projectile, the energy used to propel it, and the angle at which it is launched. Vertebrates and invertebrates alike have been successfully modelled as projectiles that are propelled by the energy from muscles (e.g. Calow & Alexander, 1973; Bennet-Clark, 1977; Alexander, 1983; Emerson, 1985; Vogel, 1988).

It would be surprising if the process of divesting oneself from one's skeleton and expanding and hardening a new skeleton had no effect on locomotor ability. Perhaps because jumping is relatively tractable to analysis, most of the studies of moulting and locomotion that exist concern jumping insects (Gabriel, 1985a, b; Queatham, 1991; Katz & Gosline, 1992, 1993), although reports regarding lobsters (Cromarty, Cobb & Kass-Simon, 1991) indicate that the effects of the moult cycle apply more generally than to jumping insects alone. For the locust *Schistocerca gregaria*, Gabriel (1985a, b) demonstrated that there is a two-fold difference in jumping ability between animals on the first day of an instar and their day of peak jumping ability, but did not attempt to interpret within-instar changes in jumping ability using ballistic models. The ballistics equations provide a mechanical model integrating data on mass, jump angle and force production to yield biomechanical predictions about how the physiological changes associated with the moult cycle should act separately or in concert to affect locomotor performance in jumping arthropods. These equations therefore provide a framework for quantifying which factors are most important in determining jumping ability during ontogeny.

Jumping ability (measured as the horizontal distance an animal can jump) varies regularly with the moult cycle as development progresses in juveniles of the acridid grasshopper, *Schistocerca americana* (Acrididae: Cyrtacanthacridinae). At the beginning of each instar, jumping ability is low. Jumping ability increases to a maximum 2–5 days into each instar, then decreases again before the next moult (Queatham, 1991). This pattern cannot be explained as a simple inability to jump on the day of the moult, as jumping ability changes continuously throughout the entirety of the instar. Presumably, its causes lie in the many changes that take place concurrently over the course of the moult cycle, but the relative importance of factors such as increasing body mass or alterations in force production during the moult cycle has not been investigated explicitly. Rather, data collected to date concerning changes in force production and body mass during

development have been interpreted using linear, continuous scaling models, despite the stepwise, discontinuous nature of arthropod development (Katz & Gosline, 1992, 1993).

This study focuses on the jumping ability of the sixth or penultimate instar in *Schistocerca americana*. Queathem (1991) hypothesized that jump energy and body mass could explain the variation in jumping ability within an instar. Ballistics equations predict that changes in body mass should cause changes in jumping ability. The ratio of jump energy to body mass should be mirrored by changes in jump ability, if the angle of take-off for maximum jumps does not vary over the instar. Jump energy will be directly proportional to ground reaction force production, if little energy is lost to drag and rotation of the body. Developmental changes in both muscle and skeletal function could result in changes in force production. If muscle growth occurs or the skeleton becomes stiffer over time, the peak forces produced by the jumping leg might be larger, offsetting the effects of a larger body mass. Here, we address several hypotheses by determining force production and the motion of the grasshopper's body to define the factors responsible for ontogenetic changes in jumping ability within an instar.

Methods

Animals

Individual *Schistocerca americana* (Acrididae: Cyrtacanthacridinae) were marked on the day of their moult to instar 6 (the last instar before adulthood) and housed 4 to a container in Mason jars with mesh lids placed next to 40 W light bulbs on a 12:12 light/dark cycle. During the daytime, the temperature inside the jars was 30°C. Animals were fed alfalfa sprouts and lettuce *ad libitum*.

Performance tests

Each animal was made to jump 3–5 times every day until it moulted to adulthood. The jump that covered the greatest horizontal distance was used as an indicator of that animal's best performance on that day. Animals were induced to jump by startling them or, if necessary, touching them gently. The horizontal distance between a grasshopper's head in the starting position before a jump and where its head touched the ground following a jump was measured with a metre stick and defined as jump distance.

Ground reaction force

We measured ground reaction forces using a miniature force platform (Full & Tu, 1990) modified to measure vertical, horizontal and lateral forces simultaneously. The jumping surface measured 10.7 × 6 × 0.06 cm and was constructed of model aircraft plywood and mounted on 4 brass beams. Semiconductor strain gauges (Micromasurements Inc.) were bonded to spring blades cut from the brass supporting beams at each corner of the platform. Loads in the range of 0.001 to 1.0 N produced a linear response with a maximum variation across the platform of less than 7%. In most cases, the animal jumped from the centre of the platform, so that the variation across the platform produced little error.

Cross-talk between vertical and horizontal outputs was less than 2%. Vertical to lateral cross-talk was the largest at 11%, but this error was reduced 2–5% by a correction factor based on calibrations. Test signals were digitally filtered using a Butterworth filter with zero phase shift. After repeated testing, we selected a cut-off frequency of 210 Hz (unloaded natural frequency of the platform was 400–650 Hz). This cut-off frequency did not result in amplitude modulation or loss of any signal components.

Signals from each force platform channel were amplified (Vishay Measurements Group) and collected by an analogue to digital converter (C-100, Cyborg) interfaced with a computer (IBM PC/AT). Force signals were sampled at a frequency of 1000 samples/sec.

The 10 consecutive milliseconds of peak force production during a jump were chosen by locating the maximum value through visual inspection, and averaging that value with the 4 or 5 readings before and after it. Subsampling indicated that shifting the sample 2 or 3 milliseconds to either side of its chosen value would not have changed the results significantly.

Kinematics

Each jump was taped using a video camera (Video Logic CDR660) capturing 120 frames/sec. Jumps were filmed from the side to capture the animal's trajectory. Single video fields were stored and the coordinates of the head and abdomen in each frame were digitized into a computer (IBM PC/AT) with a video analysis system (Peak Performance Technologies Inc.). These data were used to generate spatial models showing the rotation of the body in the vertical plane perpendicular to the camera.

Statistics

Statistical analyses were performed using JMP version 2 (copyright 1989 by SAS Institute, Cary, NC).

Centre of mass.

Three animals were chosen randomly at the days of lowest (day 1) and highest (day 11) average body mass, and frozen in the approximate position from which grasshoppers begin a jump. The major postural change during jumps is the extension of the metathoracic tibiae. As the tibiae account for less than 4% of total body mass (each tibia weighing 9–18 mg), it is unlikely that their movement could significantly alter the location of the centre of mass. Frozen animals were photographed in lateral view while hanging from a thread attached to a tiny hole perpendicular to the midline of the animal (Alexander, 1983: 13). Each animal was photographed suspended from 2 points. The photographs were used to extend the vertical line of the thread through the body of the animal from each suspension point. The centre of mass was located where the 2 lines intersected in the vertical plane longitudinally bisecting the body.

Results

Ground reaction force

Within a single jump, force production rose from zero to a peak almost linearly through time (Fig. 1). The force profile was right-skewed throughout the instar. The time of force development did not change during the course of the instar, but profiles varied in magnitude on different days of the instar. Peak force production ranged from 8.2 to 16.3 times body weight.

The ground reaction force vector angle was relatively constant throughout take-off and averaged 45° (representative force loop shown in Fig. 2). The angle of the force vector during the 10 msec of peak force production did not change over the course of the instar and did not differ significantly from 45° (Fig. 3).

Kinematics

Animals tended to pitch counter-clockwise, as viewed from their right, on the first day of instar six, tilting their heads upward (Fig. 4a). Rotation in this direction also occurred on the days of maximum jump distance and maximum force production, but through a larger arc, so that animals on these days often rotated 180° or more (Fig. 4b, c). On the last day of the instar,

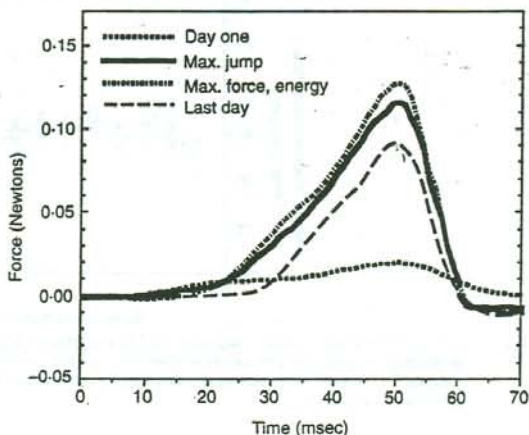


FIG. 1. Jump force profiles. Jump force first rose to a peak and then declined rapidly during each jump impulse. The magnitude of the force impulse changed over developmental time, but the basic shape of the profile and the time course of force production did not change.

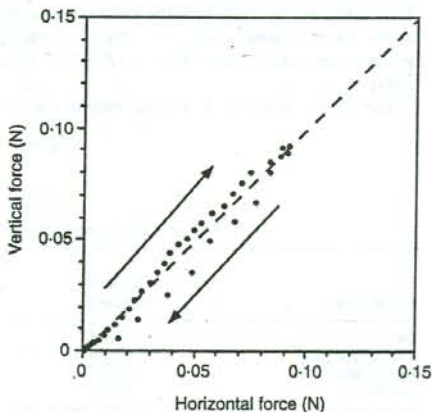


FIG. 2. Force loop during instar six. This is a representative plot of vertical force against horizontal force that shows how the angle of the force vector changed during jump force production. A line drawn from the original through a point on the plot has the same angle as the force vector at that point. The loop is traversed clockwise over time.

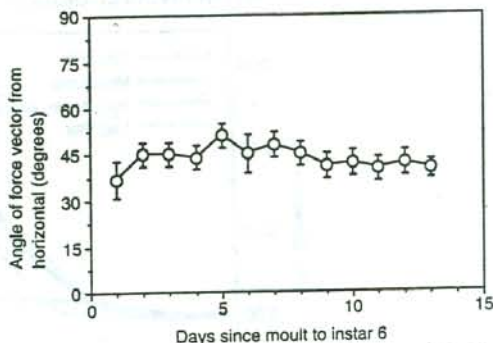


FIG. 3. Force vector angle during instar six. The average angle of the force vector during the 10 msec of peak force production did not change over the course of the instar, and did not differ significantly from 45 degrees. Symbols represent means \pm one standard error, with sample sizes ranging between four and 15 jumps, no more than one jump from any individual on a given day.

rotation resembled that of the first day (Fig. 4d). Backward rotation thus occurred throughout the instar. Angular velocity did not differ among days (Table I). This meant that the angle through which an animal rotated was correlated with how long the animal spent in the air ($r^2 = 0.59$).

The location of the centre of mass changed during the instar (Fig. 5). On the first day of the instar, the centre of mass was located anterior to the joint between the metathoracic coxa and femur, whereas by the end of the instar, the centre of mass had moved to a point almost directly above the coxa-femur joint. The centre of mass thus moved 1.52 mm posteriorly ($P < 0.0005$, pooled t -test) and 0.27 mm dorsally ($P < 0.01$, pooled t -test) between the first and last days of the instar.

The kinetic energy of a rotating body is expressed by the following equation:

$$E_k = 0.5 I \omega^2 \quad (1)$$

TABLE I
Head-up pitching (backward rotation) of body during jumping

Day of instar	N	Rotation (degrees) ^a	Initial angular velocity (rad/sec) ^a	Moment of inertia I (kg m ²) ^b	Kinetic energy E _k (mJ) ^{b,c}
Day one	3	45 (80)	5 (8)	2.24×10^{-7}	0.003
Day of max. jump	7	161 (90)	14 (5)	3.55×10^{-7}	0.035
Day of max. force	4	108 (35)	10 (3)	6.38×10^{-7}	0.032
Last day	5	96 (62)	15 (10)	7.09×10^{-7}	0.080

^a Mean (standard deviation); 1 jump per individual

^b Calculated from mean values of length and mass

^c Calculated for a slender rod using mean values of I

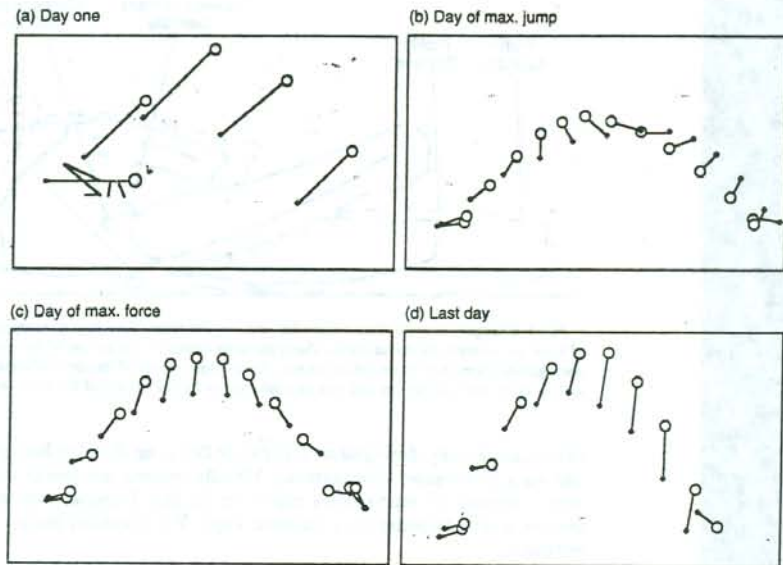


FIG. 4. Body rotation during jumps during instar six. These representative spatial models for four individuals show that backward rotation occurred throughout the instar. The apparent lengthening and shortening of the body is caused by rotation in a plane not perpendicular to the camera and/or a small lateral component to the jump. Figure size is normalized to jump distance.

where E_k is kinetic energy, I is the moment of inertia, and ω is angular velocity. Modelling the grasshopper's body as a solid rod, we calculated its moment of inertia using the following equation:

$$I = 1/3 M L^2 \quad (2)$$

where M is body mass and L is the length of the body, using average values of mass and body length. We estimated the amount lost to rotation using Equation 1. Values ranged from 0.003 mJ at the beginning of the instar to 0.08 mJ towards the end (Table I).

Maximum jump distance, force, jump energy and body mass

Instar six lasted an average of 13 days, with a standard error of 0.5 days. For the first three days of the instar (Stage I), jump distance, force production, jump energy and body mass all increased simultaneously (Fig. 6). On days 3–8 (Stage II), jumping ability remained constant, while force production, jump energy and body mass increased. During days 8–11 (Stage III), jump distance decreased while force production and jump energy remained constant and body mass continued

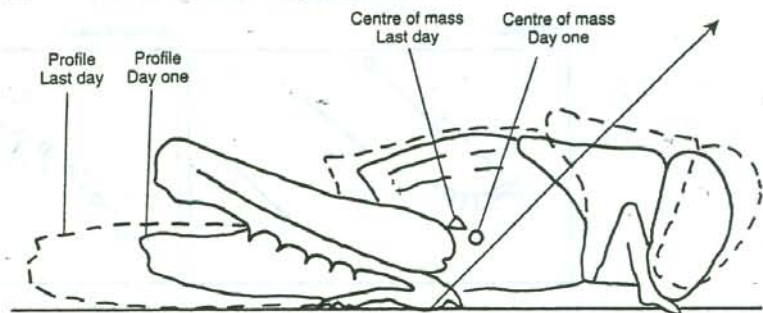


FIG. 5. Change of location of the centre of mass during instar six. The solid outline represents an individual on day one of instar six, whereas the dotted outline shows the same animal on the last day of the instar. Tracings were made from photographs taken from the animal's right side. The average location of the centre of mass relative to the coxa is marked with an open circle for day one and with an open triangle for the last day of the instar ($n = 3$ for each day).

to increase. Finally, during days 11-13 (Stage IV), jump distance, force production, jump energy and mass all decreased concomitantly. Visually assessed increases or decreases in each variable were confirmed by least-squares regression on day. Increases were marked by a significant positive slope, decreases by a negative slope. We calculated jump energy by the following equation:

$$E = \frac{mgd}{2 \sin 2\theta} \quad (3)$$

where E is jump energy or work in millijoules, m is total body mass in grams, g is acceleration due to gravity, d is the horizontal distance jumped in metres, and θ is the angle of the jump from horizontal (Bennet-Clark, 1975). Jump energy was highly correlated with force production ($r = 0.89$).

The amount of energy or work that goes into a jump can also be expressed as the product of the force produced by the animal during the jump impulse (f) and the distance through which the force is exerted (s), as follows:

$$E = f s \quad (4)$$

If jump angle equals 45° , $2 \sin 2\theta$ is equal to 2, and equation 3 may be written thus:

$$d = \frac{2E}{mg} \quad (5)$$

or, since $E = f s$,

$$d = \frac{2 f s}{mg} \quad (6)$$

When this equation is log transformed and rearranged, it becomes:

$$\log d = \text{constant} + \log f - \log m \quad (7)$$

TABLE II

Relationships among jump distance, jump force, and total body mass from least-squares regression analysis

log (y)	log (x)	Slope (S.E.)	Intercept	r ²	P
Jump distance	force	0.57 (0.08)	0.20	0.30	<0.0001
Jump distance	mass	-0.3 (0.1)	-1.4	0.07	0.0001
Force	mass	0.73 (0.09)	1.1	0.35	<0.0001
Jump distance	force	-1.14 (0.05)	-2.8	0.85	<0.0001
	mass	-1.17 (0.06)			

where constant is equal to $\log 2 + \log s - \log g$. Thus, because d should be directly proportional to f and inversely proportional to m , $\log d$ should be positively correlated with $\log f$ and negatively correlated with $\log m$. Jump distance, force and body mass were log-transformed to render distributions normal and variances independent of means, and least-squares linear regression analyses were performed to test the predicted relationship among these three variables. Force alone explained 30% of the variation in jump distance, and mass alone explained 7% of the variation in jump distance, when these two factors were considered independently (Table II). Force depended in part on body mass, however, as leg mass was included in body mass (r^2 for least squares regression of force on body mass = 0.35; Table II). When the data were analysed using body mass and force as covariates, 85% of the variation in jump distance was explained. Jump distance was significantly influenced by both force and mass (Table II).

Discussion

Possible explanations for observed patterns of variation in jump performance within an instar (Gabriel, 1985a, b; Queatham, 1991; Fig. 6a) include changes in body mass (m), jump angle (θ) and jump energy (E), as expressed by the following rearrangement of equation 3.

$$d = \frac{2E \sin 2\theta}{mg} \quad (8)$$

Body mass

All else being equal, jump distance varies inversely with body mass (Bennet-Clark, 1975; Gabriel, 1985a, b); thus the more an animal weighs, the shorter the distance it can jump. Queatham (1991) showed that body mass varied by more than two-fold within an instar for the grasshopper, *Schistocerca americana*. The present study confirms the strong negative effect of body mass on jumping ability (Table II). Body mass increased by 2.4-fold over the course of an instar (Fig. 6). Changes in body mass alone, however, were inadequate to explain the variation in jump distance. If jump angle was 45° and jump energy held constant, then equation 8 predicts only a decrease in jump distance during instar six for all but the last two days of the instar.

Jump angle

The distance a projectile will travel depends on its take-off angle. Jump distance is maximized at a take-off angle of 43°, when drag is considered, for an animal the size of a grasshopper (Vogel, 1988: 296). The angle of the ground reaction force vector from horizontal should reflect the angle

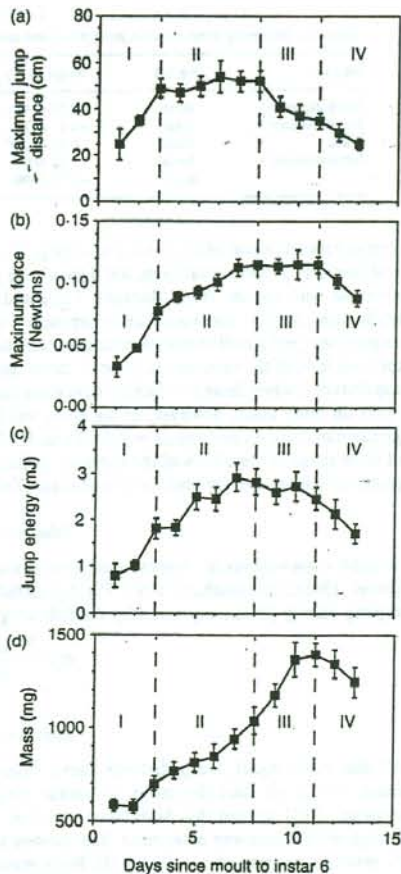


FIG. 6. (a) Jump distance, (b) jump force, (c) jump energy and (d) body mass during instar six. During the first three days of the instar, or Stage I, jump distance, force production, jump energy and body mass all rose simultaneously. During days three through eight (Stage II), jump distance levelled off, while force production, jump energy and body mass all continued to increase. Days eight through 11 (Stage III) were marked by a decline in jump distance while jump force and energy levelled off and body mass continued to rise. For the last few days of the instar (Stage IV), all parameters declined.

of take-off. Resultant ground reaction forces in *Schistocerca americana* increased linearly during the take-off period for all jumps throughout the instar, despite variation in the magnitude of the forces (Fig. 1). Magnitudes of vertical and horizontal force were approximately equal during the take-off period resulting in an angle of near 45° (Fig. 2). The angle of the resultant ground reaction force did not vary over the period of instar six (Fig. 3). Jump take-off angle therefore could not explain any of the variation in jump distance observed during growth.

Jump energy and its relationship to force production

The present results support the contention of Queathem (1991) that both body mass and jump energy interact to determine jump distance. To calculate jump energy Queathem (1991) assumed a take-off angle of 45° which is supported by the present data (Fig. 3). Queathem (1991) speculated that changes in jump energy during the instar were the result of changes in force production (see equation 4). Jump energy would mirror changes in force production over the instar, if take-off distance(s) were unchanged and losses to drag and body rotation were minimal.

Animals lose varying amounts of energy to drag once they are in the air. Thus jump efficiency (the ratio of the height of a jump in air to its height *in vacuo*) ranges from 0.4 to 0.9 for a flea, or from about 0.6 to almost 1.0 for *Schistocerca gregaria* larvae, depending on drag (Bennet-Clark & Alder, 1979; Bennet-Clark, 1980). The drag acting on a body with a Reynolds number (*Re*) of about 3000, similar to that of a jumping grasshopper, depends on the body's effective frontal area normal to the direction of motion and on its drag coefficient, which depends in turn on its shape (Vogel, 1977; Bennet-Clark, 1980). If grasshoppers can control their attitude while in the air, and if they jump so as to maximize the horizontal distance between their origin and their landing place, then perhaps they should orient their bodies at an angle of attack that would maximize the ratio of lift to drag forces (Norberg, 1985: 133). Bennet-Clark (1980) noted that grasshoppers can control their body attitude during take-off, but fail to alter the angle during the flight phase. In the present study, grasshoppers spent much of the jump oriented normally to the direction of motion regardless of which day during the instar was considered (Fig. 4), so they could not have minimized energy losses to drag by their posture during the time when jump distance was the greatest. Wind tunnel studies are necessary to determine the effects of mid-air rotation on drag and lift, and thereby on jump efficiency, but Bennet-Clark's estimates indicate that losses to drag for grasshoppers of this size are in the order of 10 to 20%.

Click beetles have been shown to lose 40–50% of their jump energy to rotation of the body (Evans, 1973). Whether there are any energetic losses to rotation will depend on the magnitude and direction of the ground reaction force vector. The greater the perpendicular distance between the centre of mass and the ground reaction force vector, the greater the turning moment, and the more energy that will be lost to rotation instead of being used in propulsion. If the centre of mass moves, because some parts of the body expand more than others during growth, then the jump force vector might pass through the centre of mass during some periods of the instar, but not others. The result would be ontogenetic differences in the amount of jump energy lost to rotation. We originally hypothesized that movement of the centre of mass might accompany within-instar growth, as the grasshopper's abdomen appears to be much more extensible than the thorax, which could favour weight gain posterior to the legs. The centre of mass did in fact move a small distance (about 1.3 mm). To prevent greater rotational energy losses the angle of the force vector would also have to change. There was no such change in the ground reaction force vector angle. If the perpendicular distance between the centre of mass and the force vector, or moment arm,

increased between the beginning and end of the instar, turning moments must also have increased (Fig. 5). On the other hand, postural adjustments made just prior to the jump might have been sufficient to compensate for this change in the location of the centre of mass. We quantified energetic losses to rotation using our data on angular velocity to determine whether such losses might be significant.

Energetic losses to rotation increased with moment of inertia and angular velocity (equation 1). Moment of inertia increased with total body mass and with the square of body length. Both these values, as well as angular velocity, were lowest on the first day of the instar, before any growth had occurred, but this was when jumping ability was also very low. Angular velocity was as high on the day of maximum jumping ability as on any other day (Table I), so changes in angular velocity cannot account for changing jumping ability. In short, we documented no changes in energy lost to rotation sufficient to explain two-fold within-instar variation in jump distance (Fig. 6). Energy losses were less than 5% of total jump energy at maximum (Table I) and not correlated with jumping ability.

At first glance, it seems baffling that animals should so consistently rotate in the air when they jump. The surfaces from which animals are generally induced to jump in the laboratory, however, are flat and horizontal. As their name suggests, grasshoppers are common in vegetation, a substratum likely to be flexible, and it is possible that behaviour which causes rotation in the laboratory might have some other effect were the grasshopper oriented vertically on a more compliant substratum. It would be interesting to know whether these animals continue to rotate during jumps from natural substrata, such as grass stems.

Effect of force production and body mass on jump distance

Because energy losses to drag and rotation were small and leg length, and probably therefore also take-off distance, does not change during an instar (Brown & Davies, 1972; Daly, 1985), jump energy was directly correlated with force production (Fig. 6b, c). When an animal jumps, it applies a force to the ground, which exerts a reaction force against the animal as the animal's leg extends. It is this force that propels the animal into the air. Many of the physiological changes that are thought to take place over the course of a single instar, such as changes in skeletal stiffness (Hepburn & Joffe, 1974; Katz & Gosline, 1992; Queatham, *In prep.*) or increases in the strength of the principal jumping muscle (the extensor tibia; Queatham, *In prep.*), should affect jumping ability. Skeletal stiffness affects jumping ability by altering the effectiveness of the limbs as levers or poles. It also affects specialized portions of the skeleton that store energy for the jump as deformation and act as cuticular springs to increase power outputs. If the extensor tibia muscle increases in mass, more energy can be provided to power the jump (Bennet-Clark, 1975). Changes in skeletal stiffness, muscle size, or both could therefore strongly affect jumping ability by altering force production. The load that must be propelled is the entire mass of the body, whereas the amount of energy available for a jump is proportional to the force that can be produced. Thus, the ratio of jump force to body mass determines jump distance, and this is reflected in the strong dependence of jump distance on both mass and force (Table II). Changes in jumping ability during an instar can best be understood by noting how force and mass change relative to one another during different stages of the instar.

Stage I. During the first three days after the moult, body mass only increased by 20%, while force production increased by 2.4-fold (Fig. 6 b, d). Even though muscle mass may not have increased, because the muscle and the cuticular spring must be connected in series, cuticular stiffness could

have important effects on grasshopper force production. Grasshoppers are small animals with short legs. Power is the amount of work or energy that can be produced per unit time, and short-legged animals can only be in contact with the ground for a short time during a jump impulse. Grasshopper power outputs must therefore be extremely high in order for them to jump as far as they do (Bennet-Clark, 1975; Gabriel, 1984). To increase power, grasshoppers store the energy produced by the muscles as deformation, mostly in heavily sclerotized cuticular structures at the distal end of each femur from which the tibia is suspended (Heitler, 1974; Bennet-Clark, 1975, 1976; Heitler & Burrows, 1977a, b, c; Heitler & Braunig, 1988). These cuticular springs can release the jump energy over a much shorter time than the time it takes the muscles to produce it. The amount of energy that will actually be stored, given that only limited deformation of the spring is possible, will be determined by the stiffness of the cuticle. Cuticular stiffness in one grasshopper species has been shown to increase throughout the instar until the last day or so before the moult (Hepburn & Joffe, 1974), which would increase the capacity of cuticular springs to store energy. Katz & Gosline (1992) described large changes in cuticular stiffness during the moult cycle, but it is not clear what effects such changes would be predicted to have on jumping ability. If the parts of the skeleton to which muscles are attached deform when the muscles contract, then the energy that goes into flexing the attachments cannot be used for locomotion; similarly, a lever that bends under loading cannot be used as effectively to do work as can one that is stiff. Consequently, stiffer skeletal elements should function better in locomotion. On the other hand, if the skeleton deforms, but the energy that goes into its deformation is returned when the structure returns to its original shape, then skeletal structures are behaving as springs, and skeletal flexibility can actually aid in increasing power outputs if resilience is high so that not much energy is lost. The resilience of the metathoracic tibia ranges from about 75% to 85% or so during the last instar before adulthood in *Schistocerca gregaria*, clearly not a large enough change to alter jumping ability by two-fold (Katz & Gosline, 1992). In any case, Katz & Gosline (1992) noted especially large changes in cuticular stiffness at the beginning of each instar in *Schistocerca gregaria*. In interspecific comparisons of adults, grasshopper cuticular stiffness and maximal jumping force have been shown to be positively correlated (Scott & Hepburn, 1976). It seems likely that, as the cuticle hardens, a greater fraction of the energy produced by the muscles can be used to propel the animal during the jump. We therefore hypothesize that the rapid increase in force production seen during Stage I is caused primarily by cuticular tanning and hardening, though muscle growth may contribute to this effect.

Stage II. During days 4–8 of the instar, body mass and force production both increased by 60%. Because mass and force production increased at the same rate, jump distance did not vary during this stage of the instar (Fig. 6a, b, d). If cuticular stiffness is responsible for the rapid change in force production during stage I, then its rate of increase must have slowed considerably by Stage II. As in Stage I, continued increase in cuticular stiffness could explain some of the increase in force production. However, at maximum, the cuticular springs will only store as much energy as the muscle has produced. Muscle mass is known in some cases to increase significantly over the course of an instar. The metathoracic dorsal longitudinal muscle in the cricket *Teleogryllus oceanicus*, for example, undergoes a 30-fold increase in mass during the last instar before adulthood (Novicki, 1989a, b). It seems likely therefore, that muscle growth is responsible for much if not all of the increase in force production seen during this stage. If muscle growth does cause this change in force production, then during this stage muscle growth must have kept pace with growth in the rest of the body as a whole, as jumping ability remained steady.

Stage III. During days 8–11 of the instar, body mass increased by 24%, while force production

did not change. Because this increase in body mass was not offset by a similar increase in force production, jump distance decreased during this stage (Fig. 6a, b, d). Presumably, neither skeletal stiffness nor muscle mass increased significantly during this period, as force production did not change. Alternatively, changes in one variable may have been offset by changes in the other, though this explanation is less parsimonious. The femur, being used in locomotion, is much more rigid than the thorax or abdomen, which comprise pieces of hard cuticle joined by thin, unsclerotized, flexible cuticular folds that make these regions relatively expandible. These data therefore suggest that although at this stage no further growth can occur within the femur, so that jump force production cannot increase, other parts of the body are not so limited, so that total body mass continues to increase.

Stage IV. The cause of the decline in force production during the last few days of the instar is obscure, but several possibilities exist.

Some change may occur just prior to ecdysis that affects the mechanical properties of the cuticle, causing it to become less stiff. This seems unlikely, as the exocuticle is the only stiff part of the cuticle, and cannot be resorbed, but must instead be shed (Uvarov, 1966; Chapman, 1982).

Some arthropods are known to undergo reductions in muscle mass just prior to ecdysis. Crabs (*Gecarcinus*) lose about 60% of the mass in the muscles of their enormous claws just before moulting, presumably to facilitate drawing a large limb through a small opening (Skinner, 1966; Mykles & Skinner, 1982; Mykles, 1992). The grasshopper femur might exhibit this phenomenon as well.

If new muscle continues to be manufactured after apolysis, when muscle attachments cease to be made, then eventually full contraction of the increasing mass of muscle might exert sufficient force to sever the attachment to the skeleton. After apolysis, these tonofibrillae, or muscle attachments, may actually be partially digested by the moulting fluid (Zacharuk, 1976), so that they are much more likely to break. Should such breaks occur, their consequences could range from an inability to jump, to disruption of the cuticular folds that make post-moult expansion possible (Hackman & Goldberg, 1987). It is certainly the case that, although individuals can jump no further on the first day of the instar than they can on the last, their willingness to jump is much greater on the first than on the last day. By the end of the instar they have become remarkably sluggish. This change in behaviour ought to be strongly favoured by natural selection if the consequences of jumping full force just prior to ecdysis were dire. Obviously, the next step in examining the causal mechanisms of variation in within instar performance is a characterization of the muscle and its cuticular attachments (Queathen, 1992).

Ontogeny and scaling

The present data on within instar variation in arthropod performance and its potential causes reveal how much remains to be understood about ontogeny. Simple scaling models that describe how morphological or performance variables change as a function of body mass can be used to make predictions about how growth should occur or what its effects should be (e.g. Katz & Gosline, 1992, 1993), but are difficult to interpret in the light of the essentially discontinuous, stepwise nature of the moult cycle. Variation in jump distance is six-fold over a 280-fold range in body mass for all ontogeny in *Schistocerca gregaria* (Katz & Gosline, 1993). Six-fold variation in jumping ability is seen within the single ontogenetic stage of adulthood. Adults on the day of their final moult can jump no higher than a first day, first instar juvenile that is one six-hundredth the adult's mass (Katz & Gosline, 1993). Thus six-fold variation in jumping ability is seen both across

all of ontogeny, where body mass varies greatly, and within a single stage, where mass varies much less. This suggests that simple linear scaling models cannot adequately describe the relationship between jumping ability and size.

Finally, our results, like all other results on locomotion and moulting to date, were obtained using grasshoppers as a model system. These results, however, are likely to be of general importance for locomotor ability in virtually all arthropods. Increases in body mass of the type documented here must certainly affect other kinds of locomotion besides jumping, as the effects of loading on locomotor performance are well known.

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